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THE SCIENTIFIC MEMOIRS

OF

THOMAS HENRY HUXLEY

Walker & Boutall ph. sc.

T. H. Huxley

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THOMAS HENRY HUXLEY

EDITED BY

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PREFACE

WHEN, after the death of the late Professor Huxley, the question of the form of a memorial to him was being discussed, among the proposals made was one to republish in a collected form the many papers which, during well nigh a half century of scientific activity, he contributed to scientific societies and scientific periodicals. It was felt that while his scientific treatises in the form of books, as well as his more popular writings, might safely be entrusted to the usual agencies of publication, there was a danger lest his exact scientific writings, scattered among many journals, might be in part overlooked or at least not gain that prominence in the eyes of students of biological science in times to come which was their due. And it was suggested that the financial responsibilities, by no means light ones, of publishing in an adequate form these collected scientific memoirs might be met out of the fund subscribed for a memorial. The Messrs. Macmillan, however, who for many years had had close relations as publishers with Professor Huxley, very generously, as a contribution to the memorial, undertook all the financial responsibilities of the republication, provided that we would be willing to bear such editorial labours as might be necessary. This of course we were delighted to do; the reprinting and the reproduction of the illustrations were at once begun, and we are now able to offer the first volume, which will be followed as rapidly as possible by the others. So far as we can judge, the work will be completed in four volumes.

The papers are arranged in chronological order, and the present volume contains fifty memoirs originally published between 1847 and 1860. The list of papers which we propose to republish (and we have done our best to make the list complete) contains about two

hundred titles, exclusive of the memoir on *The Oceanic Hydrozoa*, published by the Ray Society in 1859, which, from its size and character, we have considered as an independent publication.

Huxley produced so great an effect on the world as an expositor of the ways and needs of science in general, and of the claims of Darwinism in particular, that some, dwelling on this, are apt to overlook the immense value of his direct original contributions to exact science. The present volume and its successors will, we trust, serve to take away all excuse for such a mistaken view of Huxley's place in the history of biological science. They show that quite beyond and apart from the influence exerted by his popular writings, the progress of biology during the present century was largely due to labours of his of which the general public knew nothing, and that he was in some respects the most original and most fertile in discovery of all his fellow-workers in the same branch of science.

Older naturalists will, we feel sure, welcome this complete and convenient collection of writings which they have long known and long treasured. To our younger brethren we offer it as a most valuable mine in which searching they will find a most interesting history of the birth and growth of general ideas which seem to them now the most elementary truths of their science, while at the same time they will be brought to know models of style, patterns of sincerity and lucidity of exposition, which haply they may set before themselves as standards towards which they may strive.

As a frontispiece to the present volume we present a photograph of Huxley, taken in 1857, when he was thirty-two years of age, a time corresponding to the middle of the period covered by the memoirs contained in the volume.

Our thanks are due to the Royal, the Medico-Chirurgical, and other societies for the use made, for the purposes of reproduction, of periodicals contained in their libraries.

M. F.

E. R. L.

January, 1898.

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THE SCIENTIFIC PAPERS OF THOMAS HENRY HUXLEY

I

ON A HITHERTO UNDESCRIBED STRUCTURE IN THE HUMAN HAIR SHEATH

London Medical Gazette, vol. i. p. 1340, *July*, 1845

In Professor Henle's "Bericht ueber die Leistungen in der Histologie," for 1846, the following passage is contained :—

"Kohlrausch and Krause describe the inner layer of the sheath of the root (of the hair) which I depicted as a glossy soft fenestrated membrane, to be a layer of pale longish and flat cells, which firmly adhere in the longitudinal direction, whilst transversely they may be separated by manipulation, and then present the appearance of a membrane with irregular gaps. This same membrane separated and folded they considered to form the transverse striæ on the root of the hair. I venture to affirm that these observers have not even seen any inner layer of the sheath of the root. I beg of them to treat a hair torn out with both layers of the sheath adhering, with acetic acid ; carefully to strip off the granular outer layer, which by this means is rendered brittle, and then to adjust the focus of the microscope to the most superficial part of the hair. They will then see, not only the round holes with very even sharp borders described by me, but also, by altering the focus, they will see beneath this the transverse strips, which, as Meyer justly stated, are formed by the borders of imbricated scales. I have also at times seen a layer consisting of anastomosing longitudinal fibres, which perhaps is composed of elongated scales but I cannot say whether this was in the place of my fenestrated membrane. Certainly it is not ordinarily present."

Perhaps some light may be thrown upon the contradictory opinions here set forth, by some observations made by myself in the beginning of the present year, and since repeated so frequently, as, I hope, to avoid all source of error.

If the sheath of the root be split longitudinally with needles or a fine knife—removed, and laid out flat with the inner surface uppermost, the fenestrated membrane will be at once seen, when the focus of the microscope is adjusted to its upper surface. If some part where the sharp well-defined edge of this membrane is free, be now

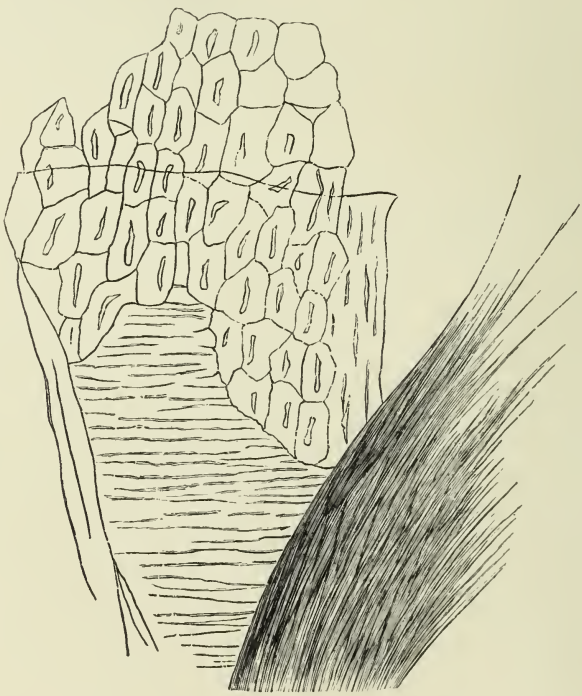


Fig i.

more carefully examined there will probably be seen extending for some little distance beyond, and lying above it, a single layer of very pale epithelium-like nucleated cells. If the eye be now carried again over the fenestrated membrane (the focus being carefully adjusted), this layer will be found to be traceable over the fenestrated membrane, and to be in close connection with it.

The individual cells composing the layer are very delicate and pale, readily escaping observation when not separated from the other structures ; they are more or less polygonal or rounded, 1-600th to

1-1200th of an inch in diameter; they are applied edge to edge or nearly so.

The nuclei are elongated, broader at their extremities than in the middle, and sometimes more or less prolonged at their angles; their average long diameter may be about 1-2000th of an inch, but in this respect they (as the cells) vary a good deal. They appear more or less granular, but do not present any distinct nucleolus.

Acetic acid renders both cell and nucleus extremely indistinct; the latter would sometimes appear to become corrugated after the manner of the pus corpuscles, &c.

The position of this layer of cells is between the fenestrated membrane and the cortical scales; clear proof of this is obtained when the cortical scales happen to peel off from the shaft and adhere to the inner surface of the sheath. If the focus be adjusted to them, depressing it brings into view, 1st. the layer of nucleated cells; 2nd. the fenestrated membrane.

Subjoined is a drawing of the inner surface of a hair sheath, illustrating this.

Possibly it is the layer of cells here described which has been confounded by Kohlrausch and Krause with the fenestrated membrane, which has been described by Henle as consisting of anastomosing longitudinal fibres, and by Meyer (cited in Professor Henle's "Allgemeine Anatomie," p. 295), as a stage of development of the cortical scales.

II

EXAMINATION OF THE CORPUSCLES OF THE BLOOD OF AMPHIOXUS LANCEOLATUS

British Association Report, 1847, *pt.* 2, *p.* 95

IN September last I was furnished, by the kindness of Professor Edward Forbes, with one of the living specimens of *Amphioxus lanceolatus*, which that gentleman exhibited at the meeting of the British Association at Southampton.

On the succeeding day I proceeded to examine the blood of the animal, but it unfortunately no longer exhibited any signs of life, and it was with difficulty that I obtained two drops for that purpose; the one by making an incision into the skin (having first carefully dried the surface), the other by cutting off the extremity of the tail. This difficulty will, I trust, be a sufficient excuse fòr the want of that completeness about the following statements, which more frequently repeated observations might have given them; at the same time I believe they will be found correct as far as they go.

The blood was thin and had a very slight rusty tinge. Under the microscope (objective $\frac{1}{6}$th of an inch, Ross) it presented the following appearances: in both specimens a number of large, irregular, pale greenish granule-cells, rather more than $\frac{1}{2500}$th of an inch in diameter; these contained a few scattered strongly refracting granules, were shot out into one or two irregular processes, and adhered together into masses. Besides these there were others having much the same characters, but possessing either more or fewer granules, so that there was a complete gradation exhibited from those which were full of coarse granules, to those which had quite a fine texture without any granules at all.

By the action of water the processes became obliterated, and the granules all assumed the form of a very pale and colourless globular cell, with large granules here and there, and a very pale nucleus occupying rather less than half its diameter. In one part of the field I perceived such a nucleus floating about attached only to a number of granules, which appeared bound together by an intermediate substance invisible from its transparency. The whole mass appeared to have become free by the bursting of the cell-wall, which was nowhere to be detected. In one specimen only (that obtained by puncturing the skin) I observed two roundish or slightly oval corpuscles, rather more than $\frac{1}{5000}$th of an inch in diameter, with a nucleus occupying three-fifths of that extent. This nucleus was greenish-looking, and refracted light strongly, while the cell-wall was of a pale reddish colour and exceedingly delicate, so much so that it seemed more like a reddish halo round the nucleus than a distinct structure. Altogether, with the exception of the last-mentioned corpuscles, the blood of the Amphioxus had a most remarkable resemblance to that of an invertebrate animal, and that in every particular. [This communication was illustrated by figures.]

III

DESCRIPTION OF THE ANIMAL OF TRIGONIA, FROM ACTUAL DISSECTION[1]

Zoological Society Proceedings, vol. xvii. 1849, *pp.* 30–32, *also in Annals and Magazine of Natural History, vol. v.* 1850, *pp.* 141–143

THE accompanying account of the animal of *Trigonia* was forwarded to me by Mr. Huxley, Assistant-Surgeon to the *Rattlesnake*, now surveying in the Eastern and Australian Seas, under the able command and scientific zeal of Captain Owen Stanley.

The great number, beauty and geological importance of the species of this interesting genus have made especially valuable a knowledge of the structure of its animal. Quoy and Gaimard were the first to give any account of it, and a figure and description of the animal of *Trigonia* were published from their drawings and notes in the zoological division of the Voyage of the *Astrolabe*.[2] Since then I am not aware of this curious creature having been re-observed, though much has been written respecting its systematic position. As in such a case a verification of the evidence we possess, through a new and accurate set of observations, is of almost as much importance as the description of an unobserved animal, the Zoological Society may consider Mr. Huxley's notes in the light of a valuable contribution to malacology.

Both accounts confirm the idea suggested by the shell of its position among the *Arcaceæ*, and its close affinity with *Nucula* and *Arca*. The degree of union of the mantle-lobes, and the development of siphonal tubes in this family, as among the neighbouring *Mytilidæ*, is of generic and not sectional significance.

[1] The paper is by Prof. E. Forbes. The part headed *Description of Trigonia* is written by Huxley.—*Eds.*

[2] Vol. iii. p. 476, Mollusques, pl. 78, f. 5.

I add the description of the animal given by the French naturalists for comparison :—

" L'animal a le manteau ouvert dans les trois quarts de sa circonférence inférieure. Il est frangé sur ses bords, avec de petites taches ou lunules blanches qui alternent avec des stries rayonnées. On voit, au sommet de ce manteau, les impressions denticulées de la charnière, et en avant et en arrière, les muscles qui unissent les valves. Le pied est grand, robuste, sécuriforme, très recourbé en arrière, tranchant et denticulé sur son arête, de chaque côté de laquelle sont des laciniures au tiers antérieur seulement. Il ne nous a pas paru se dilater comme dans les muscles. Les branchies sont grandes, libres, subtriangulaires, en pointe, reposant, de chaque côté de la racine du pied, leur doubles lamelles. Les palpes buccaux sont excessivement petits, réunis dans une partie de leur étendue. L'anus est à l'extrémité d'un court pédicule. La disposition du manteau et le manque de tubes rapprochent ce mollusque de celui des Nucules, dont il diffère cependant par la disposition des branchies et la brièveté des appendices de la bouche."

Description of Trigonia.

The mantle-lobes are rounded and plaited, to correspond with the ribs of the shell. The edges of the mantle are marked with white spots ; posteriorly, opposite the anus they are provided with short convex appendages. The mantle-lobes are disunited throughout, not joining until they reach the upper surface of the posterior adductor, some distance above the anus.

The gills are somewhat triangular, extending backwards almost horizontally on each side of the visceral mass. Each gill is formed of three stems, fixed at one extremity, free and pointed at the other, and giving attachment throughout their whole length, on one side to depending filaments, which become shorter as they are more posterior. The filaments are formed of a tubular horny thread, supporting on one side a broad membranous fringe. I could perceive no trace of vessels in this fringe, but it appeared to be covered by an epithelium (ciliated ?).

The mouth is placed at the anterior and superior part of the animal, between two thickish horizontal lips. The labial tentacles are two on each side, rather long, lanceolate, and slightly pectinated. The anus is placed posteriorly and superiorly between the gills, and just about the posterior adductor muscle.

The so-called "foot" is composed of two portions, an upper and

quadrilateral (properly the abdomen), and a lower pointed part (the true foot), the two being set at right angles to one another.

The first portion is sharp-edged and slightly pectinated posteriorly, marked by a groove bounded by two folded lips anteriorly. The second portion is slightly pectinated along its lower edge, pointed anteriorly, prolonged behind into a curved process, where it joins the superior portion.

Visceral mass.—The mouth opens by a very short œsophagus into a wide pyriform stomach, surrounded by a dark dendritic liver. The stomach narrows into a long intestine, which descends for the whole length of the abdomen, and forms one or two loops in the substance of the generative gland; then passes up again above the stomach, penetrates the heart, and passing between the two small lateral muscles of the foot, terminates in the anus.

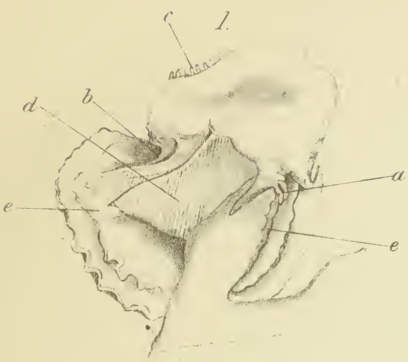
[Plate 1.][1]

Fig. (1). View of the animal with the right valve of the shell removed, and the right lobe of the mantle turned back. *a*, mouth; *b*, anus; *c*, filamentous appendages of mantle; *d*, gill; *e*, grooved superior part of foot.

Fig. (2). View of the animal from behind, with the valves separated. Letters as before.

Fig. (3). Visceral cavity laid open. *a*, stomach, surrounded by the liver; *b*, intestine; *c*, heart; *d*, generative gland.

[1] The word Plate accompanied by a number and printed within brackets refers throughout to the plate-number assigned to each plate in the present reprint of Huxley's papers, and not to the original numbering of the plates as published in transactions or journals.—Eds.



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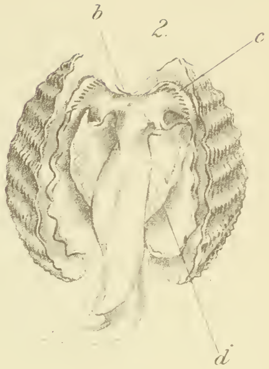

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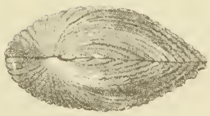

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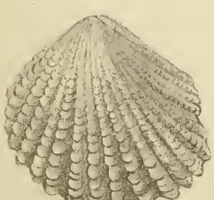

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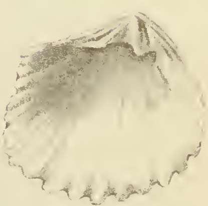

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T.H.Huxley
W.H.Baily

1 2 3. Trigonia Pectinata p 32
4 5 6 Trigonia Jukesii

IV

ON THE ANATOMY AND THE AFFINITIES OF THE FAMILY OF THE MEDUSÆ

Philosophical Transactions of the Royal Society, 1849, *pt.* 2, *p.* 413.

1. Perhaps no class of animals has been so much investigated with so little satisfactory and comprehensive result as the family of the *Medusæ*, under which name I include here the *Medusæ*, *Monostomatæ*, and *Rhizostomidæ*; and this, not for the want of patience or ability on the part of the observers (the names of Ehrenberg, Milne-Edwards, and De Blainville are sufficient guarantees for the excellence of their observations), but rather because they have contented themselves with stating matters of detail concerning particular genera and species, instead of giving broad and general views of the whole class, considered as organized upon a given type, and inquiring into its relations with other families.

2. It is my intention to endeavour to supply this want in the present paper—with what success the reader must judge. I am fully aware of the difficulty of the task, and of my own incompetency to treat it as might be wished; but, on the other hand, I may perhaps plead that in the course of a cruise of some months along the east coast of Australia and in Bass's Strait I have enjoyed peculiar opportunities for investigations of this kind, and that the study of other families hitherto but imperfectly known, has done much towards suggesting a clue in unravelling many complexities, at first sight not very intelligible.

3. From the time of Peron and Lesueur downwards, much has been said of the difficulties attending the examination of the Medusæ. I confess I think that they have been greatly exaggerated; at least with a good microscope and a good light (with the ship tolerably

steady), I never failed in procuring all the information I required. The great matter is to obtain a good *successive* supply of specimens, as the more delicate oceanic species are usually unfit for examination within a few hours after they are taken.

SECTION I.—*Of the Anatomy of the Medusæ.*

4. A fully-developed Medusa has the following parts :—1. A disc. 2. Tentacles and vesicular bodies at the margins of this disc. 3. A stomach and canals proceeding from it; and 4. Generative organs, either ovaria or testes. The tentacula vary in form and position in different species, and may be absent; the other organs are constantly present in the adult animal.

5. Three well-marked modifications of external structure result from variations in the relative position of these organs. There is either—1st, a simple stomach suspended from the centre of a more or less bell-shaped disc, the disc being traversed by canals, on some part of which the generative organs are situated, *e.g. Geryonia*, *Thaumantias*; or 2ndly, a simple stomach suspended from the centre of a disc; but the generative organs are placed in cavities formed by the pushing in, as it were, of the stomachal wall, *e.g. Aurelia*, *Phacellophora*; or 3rdly, the under surface of the disc is produced into four or more pillars which divide and subdivide, the ultimate divisions supporting an immense number of small polype-like stomachs; small apertures lead from these into a system of canals which run through the pillars, and finally open into a cavity placed under the disc; the generative organs are attached to the under wall of the cavity, *e.g. Rhizostoma*, *Cephea*.

6. To avoid circumlocution I will make use of the following terms (employed by Eschscholtz for another purpose) to designate these three classes, viz. Cryptocarpæ for the first, Phanerocarpæ for the second, and Rhizostomidæ for the third.

7. In describing the anatomy of the Medusæ it will be found most convenient to commence with the stomach, and trace the other organs from it.

Of the Stomach.—This organ varies extremely both in shape and in size in the Cryptocarpæ and Phanerocarpæ. But whatever its appearance, it will be always found to be composed of two membranes, an inner and an outer. These differ but little in structure; both are cellular, but the inner is in general softer, less transparent, and more richly ciliated, while it usually contains but few thread-cells. The outer, on the other hand, is dense, transparent, and either dis-

tinctly cellular or developed into a muscular membrane. It may be ciliated or not, but it is usually thickly beset with thread-cells, either scattered through its substance or concentrated upon more or less raised papillæ developed from its surface.

8. I would wish to lay particular stress upon the composition of this and other organs of the Medusæ out of *two distinct membranes*, as I believe that it is one of the essential peculiarities of their structure and that a knowledge of the fact is of great importance in investigating their homologies. I will call these two membranes as such, and independently of any modification into particular organs, "foundation membranes."

9. When the stomach is attached to the disc, the outer membrane passes into the general substance of the disc, while the inner becomes continuous with the lining membrane of the canals. There is a larger or smaller space between the inner aperture of the stomach and the openings of the canals, with which both communicate, and which I will therefore call the "common cavity."

10. In the Rhizostomidæ the structure of the stomachs is fundamentally the same, but they are very minute, and are collected upon the edges and extremities of the ramuscules of a common stem; so that the Rhizostomidæ, *quoad* their digestive system, have the same relation to the Monostome Medusæ as the Sertularian Polypes have to the Hydræ, or the Coralline Polypes to the Actiniæ.

11. If one of the ultimate ramuscules be examined, it will be found to consist of a thick transparent substance, similar in constitution to that of the mass of the disc, through which there runs, nearer one edge than the other, a canal with a distinct membranous wall ciliated internally. From this "common canal" a series of parallel diverticula are given off at regular intervals, and run to the edge of the branch, where they terminate by rounded oblique openings. It is not always easy to see these apertures, but I have repeatedly satisfied myself of their presence by passing a needle or other delicate body into them, figs. 28, 29.

12. The difficulty in seeing the openings arises in great measure from the presence of a membrane which surrounds and overlaps them, and being very irritable, contracts over them on being touched. The membrane consists of two processes, one from each side of the perforated edge of the branch, fig. 28. In *Rhizostoma* these two processes generally remain distinct, so that their bases form a common channel into which all the apertures open; but in *Cephea* they are frequently united in front of and behind each aperture so as to form a distinct polype-like cell, figs. 35, 36.

13. Each membranous process is composed of two membranes; the outer of these is continuous with and passes into the thick transparent outer substance above mentioned (11); the other is less transparent, more richly ciliated, and continuous with the lining membrane of the canals through the apertures. The two membranes are continuous at the free edge of the fold, and are here produced into numerous tentacula. The latter are beset with great numbers of thread-cells, and are in constant motion while the part retains its vitality,[1] fig. 29.

14. *Of the Disc.*—In the *Medusæ monostomatæ* the outer membrane of the stomach is, as I have said, continuous with the thick transparent mass of the disc, as the inner membrane is with the lining membrane of the canals which traverse it. The disc, therefore, is composed of two membranes inclosing a cavity variously shaped.

15. I have examined the minute structure of the disc in *Rhizostoma.* The outer surface of the transparent mass is covered with a delicate epithelium composed of polygonal nucleated cells joined edge to edge. Among these there are many thread-cells. Beneath this there is a thick gelatinous mass which is made up of an apparently homogeneous substance containing a multitude of delicate fibres interlacing in every direction, in the meshes of which lie scattered nucleiform bodies. On the lower surface of the disc, the only difference appeared to be that the epithelium was replaced by a layer of parallel muscular fibres.

16. It might be said that the gelatinous substance here described is a new structure, and not a mere thickening of the outer membrane; but a precisely similar change is undergone by the outer membrane in the Diphydæ, and here it can be easily traced, *e.g.* in the formation of the bracts and in the development of muscular fibre in the outer wall of the common tube.

17. The structure of the inner membrane of the disc and its canals resembles that of the corresponding tissue in the stomach, &c., but in the ultimate ramifications of the canals it becomes more delicate.

In these points there exists no difference between the Monostome and Rhizostome Medusæ.

18. The three divisions, however, vary somewhat in the arrangement of the cavities and canals of the disc.

[1] M. Milne-Edwards, in his "Observations sur la Structure de la Méduse Marsupiale," describes the fringe and its tentacles, but having altogether overlooked the true digestive apertures, he ascribes to the tentacles the function of villi. "Les franges qui garnissent les bras des rhizostomes sont donc bien certainement des organes d'absorption, et leur structure les rend en effet très propres à remplir cette fonction, qui ici dépend probablement tout entier d'un phénomène analogue à celui désigné par M. Dutrochet sous le nom d'endosmose."

In the Cryptocarpæ, the common cavity may be either small (*Thaumantias*) or large (*Oceania*); from it there proceed a number of straight unbranching canals which open into a circular canal running round the margin of the disc.

In the Phanerocarpæ the general arrangement is similar, but the canals frequently branch (*Medusa aurita*, *Phacellophora*) and anastomose in a reticulate manner.

In many of the Monostome Medusæ the centre of the under surface of the disc projects into the "common cavity" as a rounded boss (fig. 11 *a.*), and according to its form and size will seem to divide the former more or less into secondary cavities. This appears to me to be the origin of the multiple stomachs of *Medusa aurita* as described by Ehrenberg.

19. In the Rhizostomidæ, the canals of the branched processes unite and open by four (*Rhizostoma*, *Cephea*) or eight (*Cassiopea*?) distinct trunks into a wide curiously-shaped cavity, from whence anastomosing canals are given off to all parts of the disc (figs. 26, 26 *a.*). The circular vessel exists, but is not particularly obvious in consequence of anastomosing branches being given off beyond it.

20. In very many of the Cryptocarpæ (*Carybdoa*, *Oceania* (fig. 5 *a.* and *b.*), *Polyxenia*) there is a circular, valvate, muscular membrane developed from the inner and under edge of the disc. In the Phanerocarpæ such a membrane does not seem to be present, but in *Rhizostoma*, and *Cephea* it is evidently replaced by the inflexed edge of the disc fig. 26 *a.*

21. *Of the Marginal Corpuscles.*—In the Cryptocarpæ the marginal corpuscles are sessile upon the circular vessel, figs. 8, 9, 10. They are spheroidal vesicles, containing a clear fluid, and one or more spherical strongly-refracting bodies occasionally included within a delicate cell. The marginal vesicles are placed between the inner and outer membranes of the circular vessel.

In the Phanerocarpæ (*Phacellophora*) the marginal corpuscle (figs. 25, 25 *a.*) is placed at the extremity of a short double-walled tubular pedicle projecting downwards or towards the ventral surface of the disc; the under margins of the fissure in which it is lodged are prolonged into two overlapping fringes. The cavity of the pedicle is continuous with that of a canal which runs from the common cavity directly towards the corpuscle. Its walls are continuous, the inner with the inner wall of the canal, the outer with the substance of the disc. The pedicle is in fact a mere process of the system of canals, so that the position of the marginal vesicle is relatively to this system

the same as in the Cryptocarpæ. A similar remark holds good with regard to the Rhizostomidæ.

22. In *Cephea* and *Rhizostoma* the organ is placed in a notch between two lobe-like processes of the margin of the disc, and looks upwards. On the upper surface a semilunar fold extends from one lobe to the other and covers in the corpuscle; below, the edges of the lobes are thinned and overlap, figs. 33, 34.

23. There are some peculiarities in *Rhizostoma* which deserve to be noticed more fully. On the dorsal surface, behind the semilunar fold above mentioned, there is a large heart-shaped depression (fig. 33) with its base towards the corpuscle. Its surface is thrown into prominent arborescent folds, and is very richly ciliated. The deepest part of the depression is towards its base, and seems to take the direction of the base of the pedicle of the marginal corpuscle, which is just below it. I could not pass a needle from the depression into the cavity of the pedicle, but I have no doubt that they communicate, as on a lateral view the deepest part of the depression seems to project into the cavity of the pedicle. Furthermore, on pressure, the granules usually contained in the cavity of the pedicle sometimes passed into the depression.

24. Ehrenberg describes apertures in *Medusa aurita* by which the system of canals communicates with the exterior, but they are *alternate* with the marginal corpuscles, not under or above them. In *Cephea Wagneri*, again, according to Will, the canals open *beneath* the marginal vesicles. I did not observe this in the *Cephea ocellata*.

25. On the ventral surface a much slighter semilunar fold connects the base of the two lobes, fig. 34. In the centre, behind this, there is an elevation of the substance of the disc, to which the muscular bands which run along the under surface of the disc converge.

26. The canal which runs to the marginal vesicle gives off branches on each side, then opposite the base of the vesicle forms a dilatation rather larger than the cordate depression; from this a cæcal process passes off into each lobe, and so terminates. The termination of the canal in *Cephea* and *Phacellophora* is similar, but in the latter the cæca gives off lateral anastomosing branches, fig. 25.

27. In *Rhizostoma* the pedicle is somewhat bent and enlarged at its upper half. The inner membrane is richly ciliated, and the cavity which it encloses usually contains a number of rounded cell-like bodies floating about in incessant motion. There is a considerable space between the inner and outer membranes, which are thick, and therefore, when viewed by transmitted light, appear like four thick fibres.

The vesicle is about $\frac{1}{170}$th of an inch in diameter, more spherical

in small than in large individuals; it contains a closely-packed mass of strongly-refracting granules $\frac{1}{2500}$th of an inch, more or less, in diameter. The outer membrane of the pedicle can be traced over the vesicle, and the inner probably passes under it, separating the cavity of the pedicle from the vesicle: the dense mass of granules prevents this from being actually seen, but from analogy with *Mesonema*, &c., I have no doubt of the fact.

28. Ehrenberg, in his description of the *Medusa aurita*, says, "Le pédoncule est attaché à une vésicule, dans lequel on remarque, sous le microscope, un corps glanduleux, jaunâtre lorsque la lumière le traverse et blanchâtre lorsque cette dernière est réfléchie. De ce corps il part deux branches qui se dirigent vers le pédoncule du corps brun jusqu'à son petit bouton ou tête." And further on, "Le corps bifurqué placé à la base du corps brun paraît être un ganglion nerveux, et ses deux branches peuvent être regardées comme des nerfs optiques." I must confess that, judging by what I have observed in *Rhizostoma* and *Phacellophora*, it appears to me that these so-called nervous branches passing on each side of the pedicle towards its head, are nothing more than the optical expression of the thickness of the two membranes of which the pedicle is composed; and a very similar explanation may, I think, be given of his intertentacular ganglia, which appear to be nothing more than the optical expression of the thickened walls of the circular canal.

29. *Of the Tentacles.*—The tentacles of the Medusæ are of two kinds:—1, those which are processes of the outer foundation membrane alone; and 2, those which are processes of both inner and outer membranes, and therefore contain a cavity continuous with the common cavity of the body. Under the former class must be included the knob-like processes on the convex surface of many Medusæ containing thread-cells; the papillæ on the generative and stomachal membranes of *Phacellophora*; the thickened margin of the stomachal membrane in *Oceania*; the buccal tentacles of *Mesonema*; the tentacles of the fringe of *Rhizostoma* and *Cephea*, and probably the marginal tentacles of *Thaumantias*. I will proceed to describe some of these more in detail.

30. The papillæ scattered over the generative and stomachal membranes of *Phacellophora* are spherical, and connected with the membrane by a somewhat narrower neck. The substance of this, as well as of the body itself, is made up of large clear cells, but the surface of the body is covered with an immense number of round thread-cells, figs. 20, 20 *a*.

In *Mesonema*, the perpendicular membrane, which depends from

the orifice of the central cavity, is prolonged at its edges into a great number of short tentacles. Each of these is composed of an outer wall, in which immense numbers of thread-cells are imbedded, and a central axis made up of large transparent cells. This cellular axis extends for some distance beyond the base of the tentacle into the substance of the membrane, fig. 7.

31. The tentacles of the fringe of *Rhizostoma* and *Cephea* have already been described, fig. 13. The tentacles which beset the generative membrane closely resemble them, and consist of a single membrane, containing many small thread-cells, $\frac{1}{4000}$th of an inch in diameter. Their cavity is filled with a homogeneous substance, sometimes containing nuclei, similar to those of the disc (15); the inner membrane takes no part in their formation, fig. 30.

32. The marginal tentacles of *Thaumantias* are very similar (fig. 3) to the buccal tentacles of *Mesonema*; they consist of an outer membrane, in which numbers of thread-cells are imbedded, and an inner axis composed of clear cells arranged end to end; they have a peculiarity, which has been already pointed out by Prof. E. Forbes, in being placed above the marginal vesicles instead of being alternate with them, as in the nearly allied genus *Geryonia*; and from this fact, and from their totally different structure, I believe that they have a totally different origin. In *Geryonia* the tentacles belong to the second class—are processes of the circular canal; in *Thaumantias* they are simple processes of the outer foundation membrane, *i.e.* of the substance of the disc. Perhaps this difference in structure among the tentacles may turn out to be a good means of generic distinction among other members of the class.

33. As to the second class of tentacles. Such are the marginal tentacles of *Mesonema*, of *Geryonia* (Will), of *Oceania* and of *Medusa aurita* (Ehrenberg); the tentacles of the under surface of *Phacellophora*, and the interbrachial tentacles of *Cephea*.

34. In the specimens of *Mesonema* I obtained, there were not more than eight tentacles, placed at equal distances round the disc, which had attained their full development. The interval between every two was filled up by a series of bud-like rudimentary tentacles, and marginal corpuscles alternate with them. Each tentacle, in its bud-like rudimentary form, is simply a cæcal process of the circular canal, and has therefore, like it, a double wall and an internal cavity, usually filled with granules in rapid motion, produced by the ciliæ of the inner wall; the outer wall contains large thread-cells. The structure of the adult tentacle is essentially the same, but in the course of its growth it has become divided into a lower filamentous portion and

an upper dilated sac, by which it communicates with the circular canal, fig. 8.

The marginal tentacles of *Oceania* resemble these in all points; they are double-walled, communicate freely with the circular canal, and contain an immense number of minute thread-cells in their outer wall, fig. 15.

35. In *Phacellophora* there is no distinct marginal circular canal, but the sixteen radiating canals are very wide and sacciform, and communicate only by anastomosing marginal branches. Eight of the canals are narrower and run to the marginal corpuscles. The alternate eight are very much wider, and their outer, under surface is beset with a curved series of long tentacles, fig. 18. Now the lower wall of the canals is composed of the two "foundation membranes," and the tentacles are simply prolongations of these membranes; they are therefore double-walled, and contain a cavity continuous with that of the canal. At their upper part they are thicker than below, where their outer membrane is developed into spherical processes containing multitudes of thread-cells and closely resembling those on the generative membrane (30).[1] The inner cavity becomes obliterated at the lower part of the tentacle, fig. 19.

36. The large interbrachial tentacles of *Cephea* are processes of the branched arms. For the greater part of their length they have the same structure as the arms, *i.e.* consist of a dense, thick, transparent outer substance and an inner membranous wall inclosing a tubular canal; but at the extremity they are thickened, and the outer wall is raised into a number of small pyriform processes, $\frac{1}{160}$th of an inch in diameter, thickly covered with minute spherical thread-cells, $\frac{1}{5000}$th of an inch in diameter. At the same time the central canal becomes branched out into a kind of plexus, which occupies the interior of the enlarged end of the tentacle, fig. 37. These tentacles are two inches or more in length and $\frac{1}{13}$th of an inch in thickness, but other smaller tentacles, $\frac{3}{4}$ths of an inch in length by $\frac{1}{20}$th of an inch in diameter, depended from the arched concavity of the brachiferous plate. Their general structure much resembled that of the foregoing, except that the central canal terminated in a blind simple extremity, and that the pyriform bodies extended rather further up the stem.

Beside these there was a third small kind of tentacles, which appeared as small blue points among the stomachs. These were clavate bodies placed without any regular order in the axils between the stomachs, and containing an internal cavity which communicated with the nearest branch of the common canal. A series of pyriform processes, exactly resembling in form those above described, was

arranged round their hemispherical extremities. As the individual I observed was a young one (the generative organs not being developed), I conclude that these were young forms of the longer tentacles, fig. 36.

37. *Of the Generative Organs.*—It has been already noticed with regard to the Cryptocarpæ by Will (in *Geryonia*, *Thaumantias*, *Cytæis*, *Polyxenia*), and by Milne-Edwards (in *Æquorea*), that the generative organs are connected with some part of the system of canals, but they do not attempt to define the nature of this connection. I shall endeavour to do this, and to show that the generative organs, both in these and in the Phanerocarpæ and Rhizostomidæ, are always portions more or less developed of the wall of this system; and therefore consist of the two "foundation membranes," in or between which the generative elements, whether ova or spermatozoa, are developed.

38. In *Thaumantias* there are four canals radiating from the centre of the disc, at right angles to one another, and terminating in a circular vessel at the edge of the disc. Near its termination each has a rounded body seated upon it. In most of the specimens I examined this body was distended with ova, and its structure was thereby obscured; but in one instance it was replaced by an elongated, somewhat pyriform body, which on close examination was found to be simply a dilatation of the canal on which it was seated, having double walls continuous with those of the canal, only much-thickened, and a central cavity communicating freely with that of the canal. This was without doubt a young generative organ, fig. 4.

39. In *Oceania* the canals are very numerous, and radiate from the wide central cavity to the circular vessel at the margin of the disc. In young individuals these canals are narrow and nearly equal throughout, but in adults their inferior wall, for the middle three-fifths of their extent, is greatly enlarged and hangs down in folds or plaits, fig. 15. Under the microscope the wall exhibits an immense number of ova, of all sizes and stages of growth, lying in its substance; and if the edge of a fold be examined, these are seen to be placed between the inner and outer membranes. The inner membrane is thick, and composed of projecting cells with very long ciliæ; the outer membrane is dense, thinner, and much more transparent, figs. 16, 17.

40. This account agrees in its general details very closely with that given by M. Milne-Edwards of the generative organs of *Æquorea*[1]; and I regret the less not having been able to obtain male individuals, as he expressly states that in *Æquorea* the spermatozoa are developed

[1] Annales des Sciences Naturelles, t. xvi., quoted *verbatim* in Lesson's Histoire Naturelle des Zoophytes Acalèphes.

in the same position. There is, however, one discrepancy. M. Edwards states that the generative lamellæ "sont tout à fait distincts de la cavité digestive centrale." I think that on repeating his examination he would find this not to be the case. In *Oceania*, at any rate, I could readily introduce a needle from the stomach into the canals, and show that the lamellæ were mere dilatations of their wall.

In *Polyxenia*, where the canals are very short and the central cavity very large, the ova are situated in the under wall of the cavity, according to Will; but this author enters into no particulars as to the structure of the wall.

41. The generative organs of the Phanerocarpæ have been much investigated. The general result arrived at appears to be, that they are plaited tubular bands attached to the concave wall of a depression existing between the pillars of attachment of the stomachal membrane; that they are altogether separate from the central cavity; that the spermatozoa are developed in pyriform sacs opening externally, and that the ova lie free in the substance of the ovarial band.

42. The structure of the generative organs in *Phacellophora* is as follows:—The voluminous folded and plaited stomachal membrane is attached by four thick pillars to the under surface of the disc. The edges of the pillars are connected by a thin membrane, which is concave externally so as to form a sort of shallow depression or generative cavity, but the central and some of the marginal parts of this membrane are produced into long plaited processes, which hang far out of the cavity, fig. 18. Each process is a sort of sac communicating freely at its attached extremity with the cavity of the stomach, air, &c., passing readily from the one to the other. It is in fact a sort of eversion of the walls of the stomach, or more properly, of the central cavity. It consists in its upper or attached part of nothing more than the two "foundation membranes," and here they are smooth, but at their lower or free edge they become much plaited, acquire a deeper colour, and exhibit the characteristic generative elements. Short tentacles, similar to those of *Rhizostoma* (31), are scattered over the inner surface of each process, fig. 21.

43. In the *ovarium*, the two membranes develope between them immense multitudes of ova with a dark granulous yelk and clear germinal vesicle. The ova are attached to the outer surface of the inner membrane, the outer membrane passing quite freely over them, fig. 24.

44. The *testis* is similarly composed of two membranes with an intervening space. The inner membrane is produced into a vast number of thick pyriform sacs, which lie between the two membranes,

with their blind ends towards the inner surface of the outer membrane; internally, they open each by a distinct aperture on the free surface of the inner membrane.

45. The contents of the sacs are spermatozoa, and cells in every stage of development towards spermatozoa. These stages are—1. Spherical cells, $\frac{1}{1000}$th of an inch in diameter, filled with smaller nucleated cells (fig. 23 *a*). 2. Cells exactly resembling these included cells but free, and about $\frac{1}{5000}$th of an inch in diameter (*b*). 3. Similar cells, occasionally united into masses with long filiform productions (*c*). 4. Similar cells with a short process in the opposite direction also; these swim about freely and sometimes move their tails (*d*). 5. Perfect spermatozoa with elongated heads ($\frac{1}{1250}$th of an inch), rather larger below than above, where they are not more than $\frac{1}{30000}$th of an inch in diameter, with very long tails of immeasurable fineness, extending from the larger extremity (*e*). From the existence of these different stages, I conclude that the spermatozoa are formed by the elongation of the secondary cells contained in the large cells first mentioned.

46. I have not been fortunate enough to meet with any description of the generative organs of the Rhizostomidæ except that of these organs in *Cephea* by Will; and as what I have observed differs somewhat from his statements, I will describe those of *Rhizostoma mosaica* somewhat fully.

In this Acalephe, the eight arms which bear the stomachs are inserted into the lower angles of a thick square plate, which I have thence called the "brachiferous plate," fig. 27. From the upper angles of this plate there arise four pillars, of the same structure as the peduncles of the arms, and are inserted into the under surface of the disc rather external to the middle point between its centre and margin. The "brachiferous plate" has no other attachment to the disc, so that it forms the floor of an arched cavity, with four entrances between the suspending pillars of the plate.

The suspending pillars expand at their attachment to the disc into three thickened ribs or crura, two of which are lateral and external, and one central and internal: these are united by a thin membrane. The central crura meet and form a cross under the centre of the disc; the lateral crura are continuous with the substance of the disc above, and each meets with its fellow external to the centre of the disc, fig. 26. The central crura are united with these and thence with the disc by the thin membrane only. It thence follows that there exists above the central crura and the connecting membrane a wide crucial cavity; into this the canals of the suspending pillars open, and from it radiate

the canals which are given off to the circumference of the disc: the crucial cavity then is only a portion of the great system of canals.

47. The external surface of the outer half of the thin uniting membrane (which is composed solely of the two "foundation membranes"), is produced into a vast number of transverse folds of a grayish-green colour in the male, but of a deep orange-red in the female, fig. 26. These give rise to the appearance of a coloured cross shining through when the disc is viewed from above. The inner side of the folds is beset with a series of tentacles, the generative tentacles described above (31), fig. 30. In young specimens, not more than 3 inches in diameter, the generative organs were undeveloped; the outer portion of the thin membrane being as smooth as the inner, but the series of tentacles already existed.[1]

In adults the margins of the folds contain the spermatozoa in the male, the ova in the female.

48. In the *ovarium* the ova lie between the inner and outer foundation membranes, which are both ciliated on their free surfaces. The ova are attached to the outer surface of the inner membrane by a kind of pedicle, which expands into the thick vitellary (?) membrane; this chorionic coat is distinctly cellular in middle-sized ova, in larger ones it is thicker and homogeneous. If the inner surface of the inner membrane be examined, a depression will be seen opposite each ovum: the yelk of the ova is granulous and of a bright orange colour. The germinal vesicle is clear and thin-walled, and is $\frac{1}{700}$th of an inch in diameter; the germinal spot is a thick-walled cell $\frac{1}{3300}$th of an inch in diameter, fig. 32.

49. So far as the structure of the inner and outer membranes is concerned, the *testis* resembles the *ovary*. But the spermatozoa are contained in ovoid or pyriform, thick-walled sacs, about $\frac{1}{80}$th of an inch in long diameter placed between the two, fig. 31. In one individual the sperm-sacs were more ovoid in shape, and did not appear to have any particular attachment to either membrane, but in the rest they were all connected with the inner membrane, and when its inner

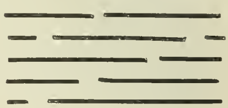
[1] It appears to me that M. Milne-Edwards must have had a young individual of *Rhizostoma* before him, when he says (Observations sur la Structure de la Méduse Marsupiale), "Nor does the plaited membrane, which forms a sort of partition between the central and the four lateral cavities, appear to be an organ of reproduction. If we examine one of these membranes superficially with the naked eye, we see towards its upper part a kind of woollen fringe, which at first sight might be taken for a series of glandular sacs, but by the aid of the microscope it is found that this appearance is due in fact to a multitude of suckers (*suçoirs*), having the greatest similarity in form to those appendages which are observable in certain parts of the body of different Zoophytes, such as *Vitella*, *Actinia*, &c. From this it would appear that these membranes are much more fitted for absorption or respiration, as is the opinion of M. Eysenhardt, than for the formation of ova."

surface was turned towards the eye, the openings of the sacs could be perceived : the sacs were filled with spermatozoa with triangular heads, about $\frac{1}{10000}$th of an inch in diameter, and very long, fine, delicate tails, fig. 31 *a*. The course of their development appeared to be as in *Phacellophora*.

50. *Rhizostoma* and *Phacellophora* then agree in having the spermatozoa developed in sacs connected with the inner " foundation membrane " and opening internally. It would appear from this that the exit for the spermatozoa is through the mouth of the animals, though this course in *Rhizostoma* would certainly be a rather circuitous one.

51. The individual of *Cephea* (*C. ocellata*) which I examined resembled, with regard to the generative organs, a young *Rhizostoma*. The line of generative tentacles was present, but the generative organs were undeveloped. According to Will, the structure of the testis in *Cephea Wagneri* closely resembles that of *Rhizostoma*. He says that there is a cavity under the disc into which the canals of the arms and disc open ; that the floor of this cavity is formed by a thin membrane covered with fine tentacular appendages, and that the band-like testes are attached to the under free surface of the membrane ; they consist of pyriform sacs (*flaschenförmigen Drüschen*) closely applied together, and each opening independently below. The spermatozoa are elongated and cylindrical, and have a very long, fine appendage.

52. With regard to the *muscular system* of the Medusæ, such observations as I have made lead me to believe that the muscular fibres are always developed in the outer " foundation membrane." In *Rhizostoma* the muscular fibres of the under surface of the disc are flat, pale, and from $\frac{1}{1250}$th to $\frac{1}{600}$th of an inch in diameter. They run parallel to one another, but the lines of separation between them are not continuous throughout, but thus : each fibre is made up of very small and indistinct fibrils, which are transversely striated, the striation being most distinct at the edge of the fibres.



53. I have not observed any indubitable trace of a *nervous system* in the Medusæ.

54. Will has described a blood-vascular system, consisting of a system of canals inclosing the water canals and containing a distinct fluid with cells floating in it. I have paid particular attention to this point in all my examinations of the Medusæ, but notwithstanding that I have had species of the very same genera (*Cydippe*, *Cephea*, *Thaumantias*) under my hands, I have never observed any trace of it. I am at a loss even to understand what he means, unless, as I strongly suspect, he has taken the outer foundation membrane, which occa-

sionally is thick and distinct from the inner, especially about the circular marginal canal, for the walls of a distinct vessel. Even if this be the case, what are the blood-corpuscles?

55. The *thread-cells* resemble in all respects those of the Diphydæ, which I have described elsewhere, consisting of a delicate outer cell inclosing another thick-walled cell, with a spiral filament of greater or less length, coiled up in its interior and capable of protrusion on pressure.

SECTION II.—*Of the Affinities of the Medusæ.*

56. Certain general conclusions are deducible from the facts stated in the preceding section. It would appear,—

1st. That a Medusa consists essentially of two membranes inclosing a variously-shaped cavity, inasmuch as its various organs are so composed (7, 8, 14, 21, 22, 29, 33, 38, 39, &c.).

2ndly. That the generative organs are external, being variously developed processes of the two membranes (38, 39, 42, 48, 49); and

3rdly. That the peculiar organs called thread-cells are universally present (7, 15, 31, 32).

Now in these particulars the Medusæ present a striking resemblance to certain other families of Zoophytes. These are the Hydroid and Sertularian Polypes, the Physophoridæ and Diphydæ, with all of which the same three propositions hold good.[1]

57. But in order to demonstrate that a real affinity exists among different classes of animals, it is not sufficient merely to point out that certain similarities and analogies exist among them; it must be shown that they are constructed upon the same anatomical type, that, in fact, their organs are homologous.

Now the organs of two animals or families of animals are homologous when their structure is identical, or when the differences between them may be accounted for by the simple laws of growth. When the organs differ considerably, their homology may be deter-

[1] "Les parois du tube nutritif sont formées d'une double membrane toujours rondée intimement dans cette partie du polype, l'externe répond aux téguments; l'interne est une continuation de la membrane digestive de la capacité alimentaire."—Cuvier, Org. de Génération des Zoophytes, Leçons d'Anat. Comp. t. viii. 2nd edit.

I have elsewhere pointed out that the same circumstance obtains among the Diphydæ and Physophoridæ.

That the generative organs are external in the Sertularian and Hydroid Polypes has been long known. Milne-Edwards has shown that they have a similar position in one of the Physophoridæ (*Apolemia*). I have observed it myself in the Diphydæ.

The presence of the thread-cells has been determined by Will in the Diphydæ, by Milne-Edwards in *Apolemia*, by myself (only??) in *Physalia*, *Physophora*, *Athorybia*, and other Physophoridæ, and in the Sertularian Polypes.

mined in two ways, either—1, by tracing back the course of development of the two until we arrive by similar stages at the same point; or, 2, by interpolating between the two a series of forms derived from other animals allied to both, the difference between each term of the series being such only as can be accounted for by the laws of growth. The latter method is that which has been generally employed under the name of *Comparative Anatomy*, the former being hardly applicable to any but the lower classes of animals. Both methods may be made use of in investigating the homologies of the Medusæ.[1]

58. A complete identity of structure connects the "foundation membranes" of the Medusæ with the corresponding organs in the rest of the series; and it is curious to remark, that throughout, the outer and inner membranes appear to bear the same physiological relation to one another as do the serous and mucous layers of the germ; the outer becoming developed into the muscular system and giving rise to the organs of offence and defence; the inner, on the other hand, appearing to be more closely subservient to the purposes of nutrition and generation.

59. The structure of the stomach in the Medusæ is in general identical with that of the same organ in the rest of the series. The Rhizostomidæ offer an apparent difficulty, but it appears to me that the marginal folds in them answer to the stomachal membrane of the Monostome Medusæ; the apertures to the inner orifice of their stomach, and the common canal to their "common cavity." Just as in a polygastric Diphyes the common tube answers to the chamber into which the stomach of a monogastric Diphyes opens; and in *Cephea Wagneri* (Will) these resemblances are still more striking. He says that each cotyledon "has at its apex a small round opening, the mouth, which leads to an ovate cavity, occupying the whole interior of the cotyledon. I consider this as the proper digestive or stomachal cavity, and believe that the cotyledons have the same relation to the vessels as the so-called suckers (*Sangröhren*) of the Diphydæ to the common tube (*Saftröhre*)."[2]

60. The disc of a Medusa is represented by the natatorial organ among the Diphydæ and Physophoridæ. Take for instance the disc of *Oceania* or *Cytæis*. It is here a more or less bell-shaped body, traversed by radiating canals, lined by a distinct membrane, united

[1] The above definitions may be thought needless and even trite, but the establishment of affinities among animals has been so often a mere exercise of the imagination, that I may be pardoned for pointing out the guiding principles which I have followed, and by which I would wish to be judged.

[2] Horæ Tergutinæ, p. 60.

by a circular canal at the margin. In the centre the radiating canals communicate freely with the chamber into which the stomach opens. The inner margin of the disc is provided with a delicate, circular, valvate membrane. The same description applies, word for word, to the natatorial organs of the Diphydæ and Physophoridæ ; the only difference being, that in the latter the stomach is *outside* the cavity (fig. 47) of the organ, instead of being, as in the Medusæ, suspended from its centre *inside*, fig. 49. And even if the different texture of the two organs should give rise to any doubt, the genus *Rosacea*, in which the natatorial organ is perfectly soft and gelatinous, furnishes the needful intermediate form.

61. The disc of the Medusæ has no representative among the Hydræ and Sertulariadæ. The cell of the Sertularian Polype rather resembles the "bract" of the Diphydæ than the "natatorial organ" in its structure and function, and in this manner the Diphydæ form a connecting link between the Medusæ and the Physophoridæ.

62. Of the two kinds of tentacles of the Medusæ, the first is represented, in the Physophoridæ and Diphydæ, by the thickenings, richly beset with thread-cells, that frequently occur in the lip of the stomach ; in the Sertularian Polypes (*Plumularia*, *Campanularia*) by the tentacles of the margin of the mouth, which precisely resemble the tentacles of the fringe of *Rhizostoma*, or the marginal tentacles of *Thaumantias*, in being composed of a single membrane covered with thread-cells, and having a cellular axis.

63. The second kind of tentacle is homologous with the prehensile organs of the Diphydæ and Physophoridæ with the peculiar clavate processes of *Plumularia*, and so far as I can judge from descriptions of their structure, with the tentacles of *Hydra*.

All the organs here mentioned commence their development as bud-like processes of the two primary membranes, elongating and attaining the forms peculiar to their perfect state as they grow older. The tentacles of the Medusæ are usually developed (as in most Monostomatæ) from the circular vessel of the disc, sometimes (*Phacellophora*) from the diverging canals, sometimes, finally, from the neck of the stomach (*Lymnorea*, *Javonia*). The prehensile organs of the Physophoridæ also have considerable variety in position. In *Porpita*, *Vitella*, *Angela* (?), they are developed from the margin of the float ; in *Physophora* and many others from the base or the pedicle of the stomach. The prehensile organs of the Diphydæ are always developed either from the base or the pedicle of the stomach. The peculiar clavate organs of *Plumularia* are developed from the common tube independently of the stomach.

64. The adult forms of these organs have all the same structure, being composed of two membranes, with a vast number of thread-cells of larger or smaller size, seated in the substance of the outer membrane or between the inner and the outer.

65. The "clavate organs" of *Plumularia* deserve especial notice, as I am not aware that they have been hitherto described, and as they exemplify in a very beautiful manner the "unity of organization" manifest among these families.

I have found them in two species of *Plumularia* obtained by the dredge at Port Curtis; they were of two kinds, the one attached to the cell of the polype, the other to the pedicle of the ovary, figs. 43, 44, 45. In each species there were three processes of the former kind, two above proceeding from near that edge of the aperture which is towards the stem, the other below from the front part of the base of the cell; they were conical in the one species, club-shaped and articulated in the other, and consisted of an external horny membrane open at the apex, and an internal delicate membrane inclosing a cavity, all these being continuous with the corresponding parts of the stem. At the apex of each, and capable of being pressed through the aperture, lay a number of thread-cells; with moderate pressure the threads only of these organs were pressed out.

I found the second kind of organ in the species with conical processes. It consisted of a stem proceeding from the pedicle of the ovary, bearing a series of conical bodies having the same constitution as those just described, fig. 45. The perfect resemblance between these and the prehensile organs of the Diphydæ cannot be overlooked.

66. The structure of the generative organs is still more instructive. In the Medusæ I have endeavoured to show that there are always processes of the two foundation membranes, the generative elements being developed between them, figs. 1 *a*, 11 *a*, 18 *a*, 26 *a*.

67. In the Diphydæ (and as I have good reason for believing in the Physophoridæ also) the generative organ commences as a simple process of the common tube (fig. 39 *a*), and undergoing great changes of form in the course of its development (*b*, *c*), it becomes at last exactly similar to an ordinary natatorial organ with a sac composed of two membranes suspended from its centre, fig. 39. In external form it greatly resembles such a *Medusa* as *Cytæis*, and this resemblance is much heightened when, as in some cases, it becomes detached and swims freely about, fig. 41. The ova or spermatozoa, as the case may be, are developed between the two membranes of the sac, the inner of which at any rate is a continuation of the inner membrane of the common tube, fig. 39.

68. The ovarium of the *Plumularia* above mentioned (65), commences as a dilatation of the apex of its pedicel, which again is a process of the common stem. It then becomes lenticular with a horny outer wall, glassy and transparent externally, but internally coloured by pigment masses. Internally it has an oval cavity communicating with that of the stem and lined by a distinct membrane, fig. 45. Between the two membranes is a thick layer of ova, more or less oval in shape, and about $\frac{1}{350}$th of an inch in diameter, with a germinal spot about $\frac{1}{2400}$th of an inch in diameter, seated in the middle of a clear space about twice that size, which doubtless represents the germinal vesicle.

69. The account given by Löwen of the generative organs of *Campanularia* differs considerably from the foregoing. After all, however, his "female polypes" may be nothing more than ovaria similar to those of *Diphyes* or *Coryne*, but having the production of tentacles from the margin carried to a greater extent than in the latter. If this be a correct explanation, the idea promulgated by Steenstrup, that there is an "alternation of generations" among the Sertularian Polypes, must be given up.

70. In *Hydra*,[1] the ova are developed in similar processes of the lower part of the body. But among the Hydroid Polypes the ovaries of *Coryne*, *Syncorine* and *Corymorpha*, as described by Sars, Löwen and Steenstrup, are most interesting. They commence as tubercles of the stem, afterwards become bodies, precisely resembling the ovaria of the Diphydæ, and finally (fig. 42) detaching themselves develope regular tentacles from their margin. The ova are formed between the two membranes of the inner sac.[2]

71. What has now been advanced will perhaps be deemed evidence sufficient to demonstrate,—1st, that the organs of these various families are traceable back to the same point in the way of development; or 2ndly, when this cannot be done, that they are connected by natural gradations with organs which are so traceable, in which case, according to the principles advanced in 57, the various organs are homologous, and the families have a real affinity to one another and should form one group.

[1] M. Dujardin, Annales des Sciences Naturelles, November 1845, states on the authority of Ehrenberg, Corda and Laurent, that the ova of the freshwater Polype are "produits dans l'épaisseur même du tissu sans ovarie ni ovule préalable."

[2] "The axis of the bell is occupied by a membranous sac, which is a prolongation of the nutritive canal, and answers to the alimentary cavity of the alimentary Polypes. The ova are developed in regular series in the interval between this alimentary capsule and the parietes of the outer sac, in an intermediate membranous sac, distinguished by its yellowish brown colour."—Cuvier, Leçons d'Anat. Comparée, t. viii. Organs de Génération des Zoophytes, p. 860. See also Duvernoy, Annales des Sciences Naturelles for November 1845.

72. Perhaps the view that I have taken will be more clear if I throw it into a tabular form, placing opposite one another those organs in the different families, for the homologies of which there is, I think, sufficient evidence, thus :—

Stomachs identical in Structure throughout.

Medusæ.	*Physophoridæ.*	*Diphydæ.*	*Sertularidæ*	*Hydræ.*
Disc	Natatorial organ	Natatorial organ.		
Canals	Canals of natatorial organ	Canals of natatorial organ.		
Common cavity... Canals of branches (*Rhiz.*)	Common tube	Sacculus and common tube	Cavity of stem.	
		Bract	Polype-cell.	
Tentacles, 1	Thickened edge of stomach		Oval tentacles.	
2	Prehensile organs		Clavate organs	Tentacles (?).
Generative organs	Generative sac		Generative organ.	Generative organ.
	Natatorial organ of generative sac			Natatorial organs (Coryne).
Marginal vesicle	?		?	?

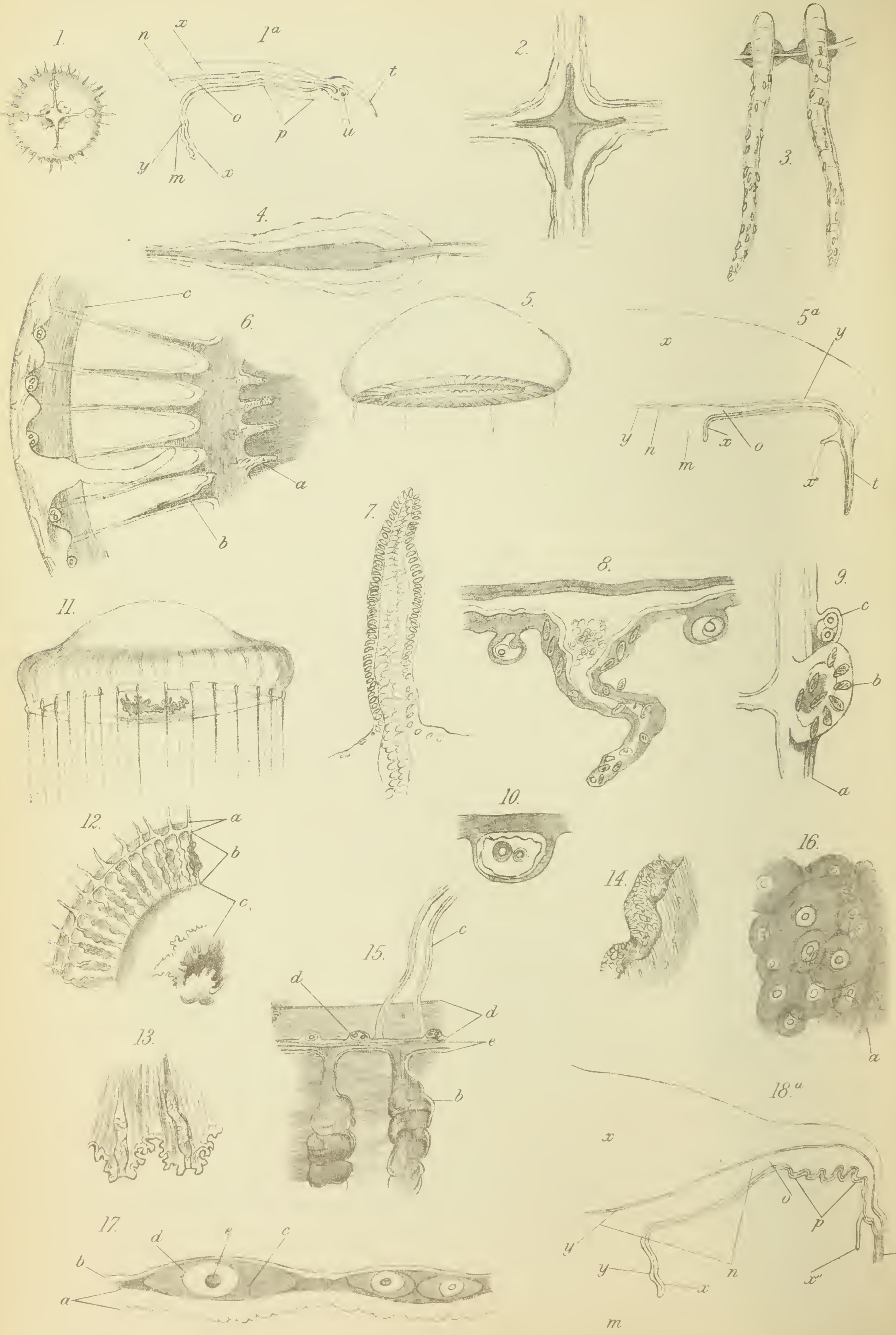
73. It appears then that these five families are by no means so distinct as has hitherto been supposed, but that they are members of one great group, organized upon one simple and uniform plan, and even in their most complex and aberrant forms, reducible to the same type. And I may add, finally, that on this theory it is by no means difficult to account for the remarkable forms presented by the Medusæ in their young state. The Medusæ are the most perfect, the most *individualized* animals of the series, and it is only in accordance with what very generally obtains in the animal kingdom if in their early condition they approximate towards the simplest forms of the group to which they belong.

74. I have purposely avoided all mention of the Beroidæ in the course of the present paper, although they have many remarkable resemblances to the animals of which it treats : still such observations as I have been enabled to make upon them have led me to the belief, that they do not so much form a part of the present group as a link between it and the Anthozoic Polypes. But I hope to return to this point upon some future occasion.

Sydney, April 24th, 1848.

*** Since the above was written I have had an opportunity (by the kindness of W. MacLeay, Esq., to whose advice I am much

[PLATE II]



indebted), of reading M. Dujardin's "Mémoires sur le Développement des Méduses et des Polypes Hydraires," contained in the Annales des Sciences Naturelles for November 1845. This author has, as it appears to me, been misled by the great analogy between the structure of a Medusa and that of the generative organ of a Coryniform Polype, into taking the detached organ of the Polype for a real Medusa. He does not hesitate to say that the Claviform Polypes are "only a first stage of development of the Acalephæ." He hints that each clavate Polype has its corresponding Acalephe, and he does not hesitate to give the latter distinct names as independent genera (*Sthenyo*, *Cladonema*).

Here, as in many other instances, the study of the Diphydæ throws light upon the matter. The detached free-swimming testis or ovary of a species of *Sphenia* has just as much claim to a distinct generic name as has *Sthenyo* or *Cladonema*, and yet in what respect does this differ from the persistent ovary of *Eudoxia*, which surely is an organ, and nothing but an organ?

Would it not be as reasonable to give a distinct name to Needham's sperm-sacs because they exhibit certain independent motions external to the body of the Cephalopod?

The point is of consequence, because it is anything but desirable that *true polypes* with *medusiform* generative organs should be confounded with the *Polypiform larvæ* of true Medusæ.

DESCRIPTION OF THE PLATES.

*** In all the sectional diagrams the letters have the same meaning, viz. *m*. Stomach. *n*. Common cavity. *o*. Canals. *p*. Generative organ. *q*. Natatorial organ. *t*. Tentacle. *u*. Marginal vesicle. *x*. Outer membrane. *x'*. Bract. *x''*. Valvular membrane.

Pl. XXXVII. [Plate 2.]

Thaumantias —— ?

Fig. 1. Disc seen from above.
Fig. 1 *a*. Imaginary vertical section.
Fig. 2. Opening of the stomach into the canals seen from above.
Fig. 3. Marginal tentacles.
Fig. 4. Young generative organ.

Mesonema?

Fig. 5. Lateral view of the animal.
Fig. 5 *a*. Vertical section.
Fig. 6. View of a segment of the disc; under surface.
a. Buccal tentacles.
b. Canals.
c. Marginal membrane (20).

Fig. 7. A single buccal tentacle much magnified.
Fig. 8. A portion of the marginal canal with a tentacle and two marginal corpuscles.
Fig. 9. Portion of the marginal canal (*a*) with young tentacle (*b*), and a marginal vesicle containing two corpuscles, each enclosed within a delicate cell-wall.
Fig. 10. A marginal vesicle highly magnified; the two corpuscles do not appear to have attained their full development, as they refract less, and the cell appears more opake.

Oceania —— ?

Fig. 11. Lateral view of the animal.
Fig. 11 *a.* Vertical section.
Fig. 12. Part of the under surface of the disc.
a. Marginal membrane.
b. Canals and generative organs.
c. Common cavity.
Fig. 13. Part of the membrane surrounding the mouth.
Fig. 14. The edge of this much magnified.
Fig. 15. Part of the margin of the disc much enlarged.
a. Marginal membrane.
b. Canal and generative organs.
c. Tentacles.
d. Marginal corpuscles.
e. Circular canal.
Fig. 16. Portion of the ovarium so folded as to have its inner membrane (*a*) outwards.
Fig. 17. Sectional view of the ovarium.
a. Inner membrane.
b. Outer membrane.
c. Ovum.
d. Germinal vesicle.
e. Germinal spot.

Pl. XXXVIII. [Plate 3.]

Phacellophora —— ?

Fig. 18. View of a segment of the under surface.
a. Marginal vesicles.
b. Tentacles in this individual very much shorter than usual.
c. Ovary or testis.
d. Buccal membrane.
Fig. 18 *a.* Vertical section.
Fig. 19. Tentacle.
Fig. 20. Portion of the buccal membrane.
Fig. 20 *a.* Round processes containing thread-cells scattered over its outer surface.
Fig. 21. Portion of the testis.
a. Generative tentacles.
Fig. 22. Sectional view of part of the testis.
a. Outer membrane.
b. Sperm-sacs.
c. Inner membrane.
Fig. 23. Stages of development of the spermatozoa (45).
Fig. 24. Ovarium.
a. Outer membrane.
b. Ova.
c. Inner membrane.

[PLATE III]

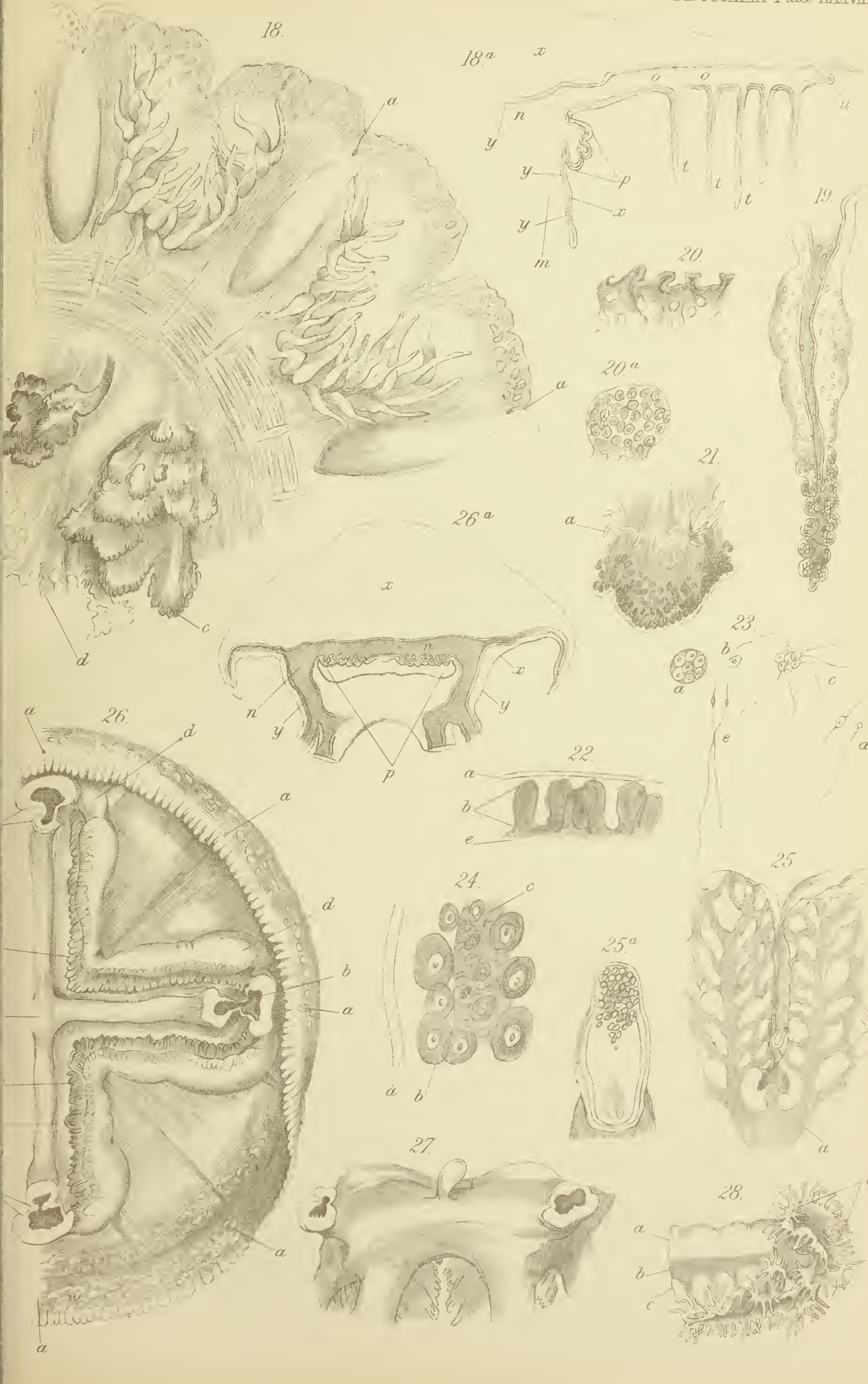


Fig. 25. Marginal vesicle from the under surface.
a. Dilatation of the canal.
Fig. 25 *a.* Marginal vesicle and pedicle very much enlarged.

Rhizostoma mosaica.

Fig. 26. View of the under surface of the disc, the brachiferous plate being cut away.
a. Marginal vesicles.
b. Cut extremity of the suspending pillar of the brachiferous plate.
c. Central crura.
d. Lateral crura.
e. Generative folds.
f. Connecting membrane.
Fig. 26 *a.* Vertical section of the Rhizostoma.
Fig. 27. Side view of the brachiferous plate detached.

Pl. XXXIX. [Plate 4.]

Rhizostoma mosaica.

Fig. 28. Extremity of one of the ultimate ramifications of the arms.
a. Thick substance of the outer membrane.
b. The central common canal.
c. The lateral canals leading to the apertures.
d. The fringes.
Fig. 29. Lateral view of one of the apertures much magnified.
a. Thick outer membrane.
b. Inner membrane.
c. Lateral canal.
d. Tentacles.
Fig. 30. Portion of the testis slightly magnified.
a. Generative tentacles.
Fig. 31. Sectional view of testis much magnified.
a. Outer membrane.
b. Inner membrane.
c. Sperm-sacs.
Fig. 31 *a.* Spermatozoa.
Fig. 32. Ovarium.
a. Outer membrane.
b. Inner membrane.
c. Ova.
Fig. 33. Marginal vesicle, upper surface.
a, *b.* Lobes connected by the arched membrane, *l.*
c. Cæca of the canal *f.*
d. Vesicle on its pedicle.
e. Cordate depression.
Fig. 34. Marginal vesicle from below, much magnified.
a a. Lobes.
b. Inferior connecting membrane.
c. Cæca.
d. Elevation of the outer membrane.
e. Muscular fibres.

Cephea ocellata.

Fig. 35. An aperture surrounded by its membrane.
Fig. 36. Portion of the extremity of an arm, with a young interbrachial tentacle (*a*).
Fig. 37. Extremity of one of the large interbrachial tentacles.

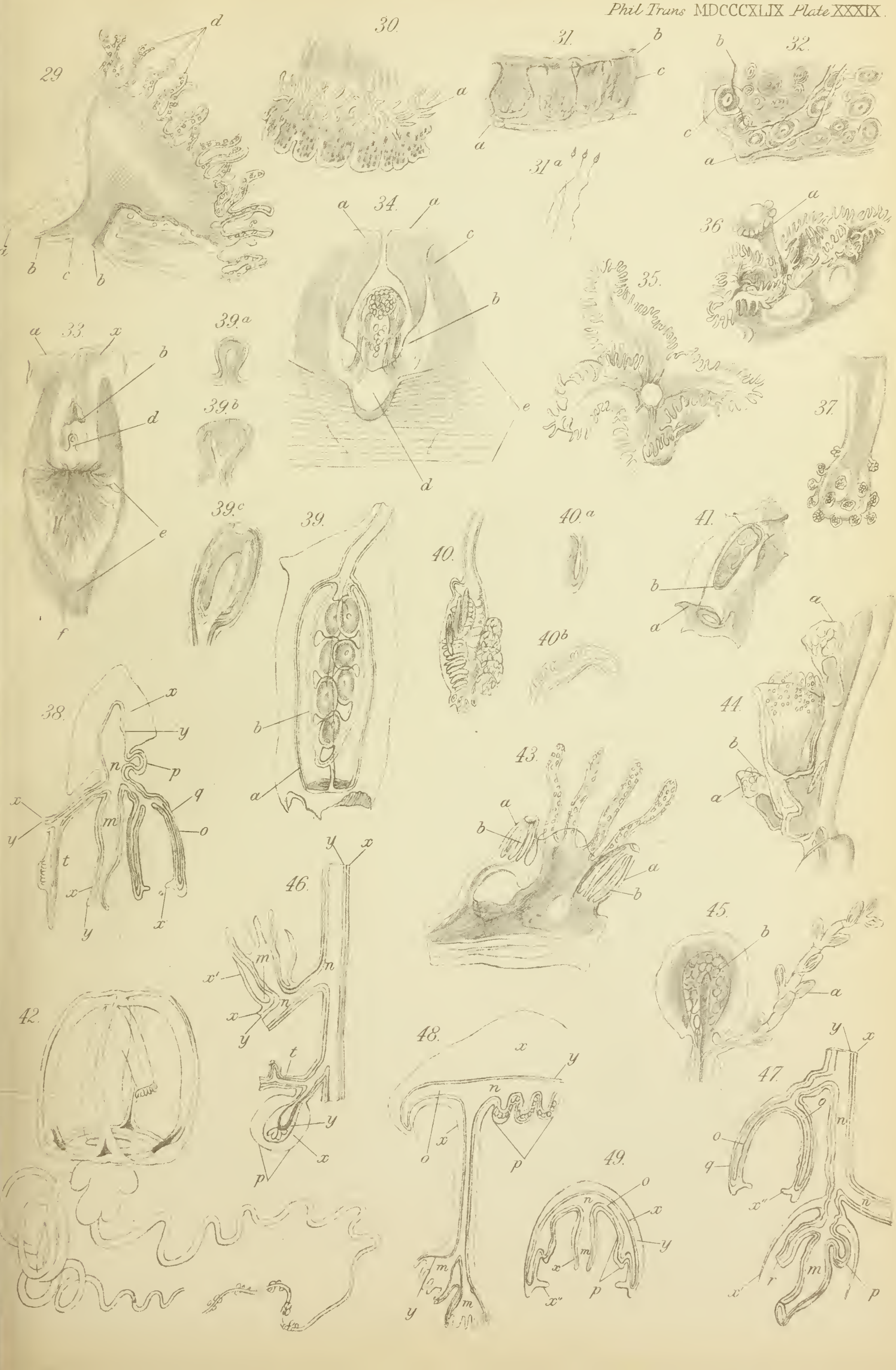
Diphydæ.

Fig. 38. Vertical section of a monogastric Diphyes.
Fig. 39. Attached ovarium.
a. Natatorial organ.
b. Ovisac.
Fig. 39 *a.* Youngest stage of ovarium.
a. Simple process of the common cavity.
b, *c.* Ovaria further advanced.
Fig. 40. Prehensile organ.
a, *b.* Early stages.
Fig. 41. Free-swimming ovarium.
a. Natatorial organ.
b. Ovisac.
Fig. 42. Free-swimming ovarium of Coryne (from Steenstrup) to compare with fig. 41.

Sertularidæ.

Fig. 43. Cell of *Plumularia* —— ?
a. Peculiar clavate organs.
b. Large thread-cells.
Fig. 44. Cell of another Plumularia, letters as before.
Fig. 45. Ovarium of fig. 43.
a. Organs containing thread-cells similar to fig. 43 *a.*
b. Ova.
Fig. 46. Section of Plumularia.
Fig. 47. Section of Polygastric Diphyes.
Fig. 48. Section of Rhizostoma.
Fig. 49. Section of Monostome Medusa.

[PLATE IV]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V

NOTES ON MEDUSÆ AND POLYPES

Annals and Magazine of Natural History, vol. vi. 1850, *pp.* 66–7

H.M.S. Rattlesnake,
CAPE YORK, *October* 1849.

MY DEAR SIR,—You will probably be interested in knowing what I have been about for the last year. I have examined (in most cases very carefully) species of the following genera of Acalephæ and Polypes: PHYSOPHORIDÆ, *Velella*, *Porpita*, *Physalia* (a good many new points), *Stephanomia*, *Athorybia*, *Agulina*, *Rhizophyra*; DIPHYDÆ, *Rosacea*, *Cuboides* (two species), *Abyla* (three species), *Enneagonea*; MEDUSIDÆ, *Sinope* (?), *Xanthea*, *Geryonia*, *Cytæis*, *Cephea*, *Oceania*, * *Bugainvillea*, *Tima*, *Aglaura* (?), *Pelagia*, * *Willsia*; POLYPES, *Tubularia*, besides some genera altogether new. The two I have marked thus * will interest you, as you describe them in your "*Naked-eyed Medusæ*." *Bugainvillea*, I may mention, has its generative organ in the thickness of its outer membrane of the stomach; *Willsia* develops bodies mostly resembling those in *Sarsia prolifera* and *gemmifera*, at the angle formed by the two first divisions of each of the four radial canals. The structure of the *Tubularia* is also very interesting. I was for a long time astonished at what appeared to be its very wide geographical distribution, until I discovered one day that it was attached in large masses to the ship's bottom!

I have found much that was new to me in all respects, but nothing that contradicted in any important matter the results at which I arrived in the paper on the *Medusæ*. On the other hand, I can speak much more confidently on some points advanced only with hesitation before. I believe that I shall be able to show you on our return evidence amply sufficient to prove,—1st, that the Hydroid and Sertularian Polypes, the Hydrostatic and ordinary Acalephæ, and the Helianthoid Polypes form one large family, which from their invari-

able and peculiar "thread-cell," I propose to call the "Nematophora"; 2nd, that this great family consists further of two subdivisions, the number of which as affixed, if we consider one subdivision, and strictly analogous and parallel if we consider the two subdivisions as thus :—

Nematophora.

Hydroidæ.	Actinidæ.
Corynidæ.	Zoanthidæ.
Sertularidæ.	Sarcoidea.
Physophoridæ.	Pennatulidæ.
Diphydæ.	Madreporidæ.
Medusidæ.	Beroidæ.

I believe that I have already evidence enough on the "Hydroid" side, but on the other I have done nothing, or next to nothing. It is a very difficult investigation, but if this intolerable heat leaves me energy enough I will do something towards it. I am unwilling to write hastily or without due evidence on this matter (especially since the establishment of my views must, as it seems to me, necessitate the total re-arrangement of the "Radiata"), and I mean therefore merely to go on making observations until we return to England. If then I find any means offer itself of publishing my results on an appropriate scale, well and good; if not, I suppose I must content myself with feeling like a "mute inglorious Hampden," and like a good philanthropist, pity the public for its loss.

I have a great advantage in the society and kind advice (to say nothing of the library) of Mr. MacLeay in Sydney. Knowing little of his ideas, save by Swainson's perversions, I was astonished to find how closely some of my own conclusions had approached his, obtained many years ago in a perfectly different way. I believe that there is a great law hidden in the "Circular system" if one could but get at it, perhaps in Quinarianism too; but I, a mere chorister in the temple, had better cease discussing matters obscure to the high priests of science themselves.

Keeping well in mind the old adage about "too many irons in the fire," I have nevertheless been able to make a few scattered observations on other animals than the Acalephæ, and I mean to embody those on the Mollusca—comet-wise—making the "*anatomy of Firola and Atlanta*" the nucleus whereunto to append a tail of observations on the genera, which will I think possess some interest, referring to the nervous system, structure of buccal mass, and the existence of a peculiar urinary system. I will send this from Sydney to the Secre-

tary of the Zoological Society, with a request that you may, if so inclined, have the first perusal of it.

Our return appears to be very uncertain, perhaps not for a couple of years. If in this remote corner of the earth I can be of any service to you either in a scientific or any other way, pray consider my best exertions as at your command. A letter addressed to me at Sydney will always reach me.

Yours very faithfully,

THOMAS H. HUXLEY.

To PROF. E. FORBES.

VI

OBSERVATIONS SUR LA CIRCULATION DU SANG CHEZ LES MOLLUSQUES, DES GENRES FIROLE ET ATLANTE

EXTRAITES D'UNE LETTRE ADRESSÉE À M. MILNE-EDWARDS

Annales des Sciences Naturelles, vol. xiv. 1850, *pp.* 193–5

AYANT navigué pendant cinq années à bord du bâtiment de *S. M. B. the Rattlesnake*, dans les eaux de la Nouvelle-Hollande et de la Nouvelle-Guinée, j'ai eu l'occasion d'étudier l'anatomie et la physiologie de beaucoup d'animaux marins. Je viens de publier un Mémoire sur la structure des Méduses, et je me propose de porter prochainement à la connaissance du public les résultats de mes recherches sur les Tuniciers ; mais j'ai pensé qu'il vous serait peut-être agréable d'apprendre dès aujourd'hui que j'ai étudié également le mode de circulation du sang chez les Firoles, dont le corps, comme vous le savez, est d'une transparence hyaline, et que j'ai obtenu ainsi une confirmation entière de vos vues relatives à la manière dont cette fonction s'exerce chez les Mollusques.

Chez la FIROLE, le cœur est placé près de l'extrémité postérieure du corps à côté de la portion redressée de l'intestin. L'oreillette est supérieure et ses parois sont composées d'un lacis de fibres musculaires striées et ramifiées, entre lesquelles on aperçoit de grands espaces ouverts. Le ventricule situé au-dessous est un sac à parois transparentes, mais fortes et denses ; il communique avec l'oreillette par un orifice garni de valvules, et donne naissance à une aorte, qui, à son origine, présente également un appareil valvulaire. Cette artère a la forme d'un tube à parois minces et transparentes ; elle fournit de suite une branche qui porte le sang à la masse viscérale (ou nucléus), formée par le foie et les organes générateurs ; puis elle se dirige en avant en décrivant diverses courbures sur le tube digestif. Parvenue sur les ganglions sous-œsophagiens ou pédieux, elle donne naissance à une artère pédieuse qui descend dans la nageoire ventrale, et s'y termine d'une manière tout à fait brusque ; son extrémité est tronquée et béante, et l'orifice ainsi formé est susceptible de se dilater beaucoup et de se contracter.

Avant de pénétrer dans le pied, ou nageoire ventrale, cette dernière artère fournit une branche récurrente qui se porte, en arrière, parallèlement à l'aorte, et se termine dans l'appendice tubulaire de l'extrémité postérieure du corps de l'animal.

L'aorte, après avoir fourni l'artère pédieuse, se dirige en avant, et se termine dans la masse buccale ; pendant ce trajet, son calibre reste à peu près le même, et l'on n'en voit naître aucune branche.

Par suite de la parfaite transparence du corps de ce Mollusque à l'état vivant, rien n'est plus facile que de suivre tout le cours du sang en circulation.—*Il n'existe point de veines quelconques.*—On voit les globules du sang sortir en foule de l'orifice terminal de l'artère pédieuse, pénétrer dans la substance du pied, et passer aussi de la masse buccale dans la grande cavité péri-intestinale ; enfin c'est par cette cavité qu'ils retournent lentement, et en s'arrêtant souvent, vers le cœur. Quelquefois on en voit qui pénètrent directement dans l'oreillette à travers les espaces inter-fibrillaires déjà mentionnés, et quelquefois aussi on voit des globules qui, pendant un certain temps, se trouvent arrêtés au milieu de ce lacis. Lorsque l'animal commence à s'affaiblir, et que la circulation se ralentit, il devient possible de suivre de l'œil un globule pendant tout son trajet à travers la cavité péri-intestinale et le cœur jusque dans l'aorte.

Dans l'ATLANTE, l'appareil circulatoire est tout à fait semblable à ce qui existe chez la Firole, si ce n'est que l'artère pédieuse en pénétrant dans le pied se divise en trois branches, dont l'une (qui correspond à l'artère récurrente de la Firole) est destinée à la portion postérieure du pied ; la seconde de ces branches se rend à la ventouse, et la troisième se porte en avant, et appartient au lobe antérieur du pied ; mais aucune de ces artères ne se ramifie, et toutes les trois se terminent brusquement par un orifice béant, à travers lequel le sang s'échappe comme chez la Firole, et se répand dans les lacunes d'alentour.

J'ai constaté une disposition analogue dans l'appareil circulatoire des Cléodores, des Crésus, observés à l'état vivant ; j'ajouterai que je me suis également assuré de l'existence d'une circulation en partie lacunaire chez divers Crustacés, tels que des Alimes, des Leucifères, des Zoés et de petits Palémons.

En résumé, je suis porté à croire que l'absence plus ou moins complète de la portion veineuse du système vasculaire, loin d'être un cas exceptionnel, est l'état normal dans la plupart des classes de la grande division des animaux sans vertèbres.

VII

OBSERVATIONS UPON THE ANATOMY AND PHYSIOLOGY OF SALPA AND PYROSOMA

Philosophical Transactions of the Royal Society, 1851, *pt. ii. pp.* 567–594*; also in Annals and Magazine of Natural History, vol. ix.* 1852, *pp.* 242–244

1. THE *Salpæ*, those strange gelatinous animals, through masses of which the voyager in the great ocean sometimes sails day after day have been the subject of great controversy since the time of the publication of the celebrated work of Chamisso, *De Animalibus quibusdam è classe Vermium Linnæana.*

In this work were set forth, for the first time, the singular phenomena presented by the reproductive processes of these animals,—phenomena so strange, and so utterly unlike anything then known to occur in the whole province of zoology, that Chamisso's admirably clear and truthful account was received with almost as much distrust as if he had announced the existence of a veritable Peter Schlemihl.

In later days an opposite fate has fallen upon the statements in question. They have been made the keystone of a revived[1] theory, and the phenomena presented by the *Salpæ* have been cited as "glaring instances" of a law governing the vast majority of the lower invertebrata—the law of the "Alternation of Generations."

2. There appeared then to be two main points to be kept in view in examining the *Salpæ*:—1st. Are the statements made by Chamisso correct? and 2ndly, if they be correct, how far is the "alternation theory" a just and sufficient generalization of the phenomena?

3. These questions, however, could not be entered upon without a thorough preliminary study of the structure of the *Salpæ*, the opportunities for which are granted but to few.

Such opportunities were afforded to the writer of the present paper at Cape York, in November 1849: for a time the sea was absolutely

[1] Not new, see (70).

crowded with *Salpæ*, in all states of growth, and of a size very convenient for examination. At subsequent periods the writer had occasion repeatedly to verify the results at which he had arrived, and to find strong analogical confirmation in the structure of *Pyrosoma* and other allied genera.[1]

4. It is proposed in the following pages to consider—

I. The structure of the species of *Salpa* examined.

II. The structure of *Pyrosoma*.

III. The homology of structure of *Salpa* and *Pyrosoma*, and of these with the ordinary Ascidians.

IV. The history of our knowledge of the *Salpæ*.

SECTION I.—*The Structure of* Salpa.

5. Before entering upon this question, there is a point of some importance to be determined, as to the upper and lower surfaces, the anterior and posterior extremities of the *Salpæ*. Observation will not decide this apparently simple matter, for as the writer has frequently seen, they swim indifferently with either end forward and with either side uppermost ; and the determinations of authors are most contradictory.

Throughout the present paper, that side on which the heart is placed will be considered as the dorsal side ; that on which the ganglion and auditory vesicle are placed, as the ventral side. That extremity to which the mouth is turned will again be considered as the anterior extremity, the opposite as the posterior. Such a view of the case appears to be more harmonious with the determinations of corresponding parts in other animals than any other. In all the invertebrata the mouth end is always considered as the anterior, the heart side as the dorsal side.

6. The two so-called species of *Salpa* examined were the *S. democratica* of Forskahl, *spinosa* of Otto, and the *S. mucronata* of

[1] Those who are acquainted with the nature of the service on which H.M.S. Rattlesnake was engaged, will readily comprehend that the author's investigations were almost *necessarily* original, and independent of anything going on in Europe.

It is the more necessary to state this, as it will be seen, in the historical part of this paper, that M. Krohn, in the Ann. des Sciences for 1846, has completely anticipated the chief results arrived at, a fact of which the author was totally unaware until his arrival in England in the end of 1850.

Still, as M. Krohn gives merely his conclusions without details or figures, his promised memoir not having appeared (so far as the writer of the present paper is aware), it is hoped that this anticipation will, by showing that perfectly independent observers arrive at the same result, rather tend to increase than to diminish any weight that may be attached to the present researches.

Forskahl, *pyramidalis* of Quoy and Gaimard. They are described by Sars as *S. spinosa* and *S. mucronata*, or rather as *S. spinosa, proles solitaria*, and *S. spinosa, proles gregaria*. This, however, begs the question as to the truth of Chamisso's theory, and I shall therefore prefer to name the two forms I observed simply *Salpa* A and *Salpa* B.

At Cape York, and only there, these two forms were always obtained together. They were of about the same size, but so totally distinct in appearance, that, had they belonged to any other genus, they would have been justly regarded as separate species.

7. *Salpa* A, Plate XV. [Plate 5], fig. 1.—The body is gelatinous, transparent, and colourless, except the nucleus (*i*), which has a deep reddish-brown tint. It has a general square prismatic shape, and is abruptly truncated and somewhat convex at each extremity. The posterior extremity is provided with eight horn-like processes, which project backwards. Two of these are short and hook-like, placed one before the other in the median line at the posterior part of the superior surface. On the upper part of the lateral surfaces there is, on each side, a short process. From about midway between the upper and lower edges of this surface, a long, conical process curves upwards and backwards ; these processes are distinguished from the others by containing a cæcal process of the system of sinuses in their base (*y*).

Close to the lower edge of the lateral surfaces there is another short process like the uppermost one.

The respiratory apertures are wide and provided with valvular lips. The posterior (*b*) is narrower, and has the valvular lip more marked.

The ganglion (*d*) is less than one-fourth of the length of the body distant from the anterior respiratory aperture.

The otolithes are four in number, hemispherical, and with a dark blackish brown coloured spot on their external surface, Plate XVI. [Plate 6] fig. 5.

The endostyle (*c*) is nearly half the length of the body (reaches as far as the sixth muscular band, counting from before backwards).

The outer surface of the integument is everywhere covered with minute asperities, like little prickles.

The muscular bands (*k*) are seven in number, and, with the exception of the anterior and posterior, completely encircle the body of the animal. This form was always free and solitary.[1]

8. *Salpæ* B, Plate XV. [Plate 5] fig. 2, on the other hand, is thus characterized. The body is subovoid, smaller at the posterior ex-

[1] The statements of Meyen (*op. cit.*) to the contrary are certainly erroneous.

tremity than at the anterior (*a*); the former ends in a point, the latter in a small square facet.

The sides are flattened into several irregular facets, and the upper and lower edges are sometimes somewhat carinated. The apertures are similar in general structure to those of the form A, and the anterior and posterior extremities project considerably beyond them.

The ganglion (*d*) is placed at about one-fourth of the length of the body from the anterior extremity. The otolithes resembled those of A.

The endostyle (*c*) is not nearly equal in length to half the body; it does not extend so far back as to the third muscular band.

The outer surface of the integument is smooth.

The muscular bands (*k*) are five in number, and none of them encircle the body of the animal, the dorsal extremities being always separated by a considerable interval. This form, when young, was sometimes found in chains; the adults were always separate.

These forms, it will be observed, are widely different, and the difference is as great between the youngest forms of each as between the adults, so that they are not derived from one another by any species of metamorphosis, properly so called.

Whatever be their external differences, however, their internal organization is so similar that the same description applies to both.

9. The *Salpa*, then, may be considered as a hollow cylinder, consisting of two tunics, an external and an internal (a, β), the former (a) forming the mantle, the latter (β) the wall of the respiratory cavity. These tunics are continuous with one another at the respiratory apertures, but elsewhere they are separated by a more or less wide space.

In very young *Salpæ* this space is like the cavity of a serous sac, but in the older forms it becomes broken up into smaller channels by the adhesion of the inner and outer tunics to one another at various places, and so constitutes a system of sinuses; it may be conveniently called the "sinus system."

10. Running obliquely from behind forwards and downwards, a thickish column or band (*e*) crosses the respiratory cavity; it is hollow, and its cavity opens above and below into the sinus system. This is the "gill."

It presents an edge anteriorly and superiorly, and on each side of this, the lateral surfaces are beset with a series of small, oval, ciliated spaces. In this species the gill has but a single grand sinus running through it, and presents no appearance of vascular ramifications. The name gill has been applied to this structure somewhat

too exclusively, as there can be little doubt that the whole respiratory cavity performs the branchial function. It is proposed, therefore, to call it the *hypopharyngeal* band, on the supposition that the proper respiratory cavity of the Ascidians answers to an enlarged pharynx.

11. The muscular bands (*k*) are closely adherent to the inner tunic; they are composed of flattened fibrils, about $\frac{1}{1200}$th of an inch in diameter, which are very distinctly transversely striated, the striæ being about $\frac{1}{7000}$th of an inch apart. The bands appear to possess no sarcolemma.

12. The intestinal canal (Plate XV. [Plate 5] figs. 5 and 6) commences by a wide somewhat quadrangular mouth (*r*) opening into a flattened œsophagus, and placed at the re-entering angle formed by the hypopharyngeal band and the upper wall of the respiratory cavity. The intestine passes backwards, then becomes suddenly bent upwards upon itself, and curving slightly to the right, terminates in a wide flattened anus, close above and to the right side of the mouth (*s*).

A wide cæcal sac (*t*), given off on the left side of the intestine and bending upwards and to the right side, constitutes the stomach.

13. There is a very peculiar appendage to the intestinal canal hitherto, it is believed, quite undescribed, and consisting of a system of delicate, transparent, colourless tubes, with clear contents, arising by a single stem from the upper part of the stomachal cæcum, and thence ramifying over the surface of the intestine (5, 6, *u*), on what may be called the rectum, that is, the terminal portion of the intestine; it forms a sort of expansion of parallel anastomosing vessels, which all terminate at the same distance from the anus anteriorly, and from the bend of the intestine posteriorly, either by uniting with one another or in small pyriform cæca, Plate XV. [Plate 5] figs. 5 and 6.

Do these represent a hepatic organ, or are they not more probably a sort of rudimentary lacteal system, a means of straining off the nutritive juices from the stomach into the blood by which these vessels are bathed?

The intestine is connected with the parietes of the sinus in which it lies by innumerable delicate short threads, like a fine areolar tissue.

14. In *Salpa* A, the only other organ contained in the circumvisceral sinus, besides the intestine and "system of tubes," is a mass of clear cells (*æ*), rendered polygonal by mutual pressure, and placed at the upper and back part of the sinus; to this body the name of "elæoblast" has been given by Krohn. It has by some authors been confounded with a liver, an organ to which it certainly has no analogy whatever. The elæoblast is much larger and more conspicuous in the

young than in the adult *Salpæ*, and frequently, but not always, its cells contain an oily matter.

There would seem to be no clue either to the homology or to the function of this elæoblast. Without hazarding a conjecture, it may be remarked, as a curious fact, that these animals, so remarkable for possessing in the fœtal state a true though rudimentary placental circulation, possess an organ which in structure and duration somewhat calls to mind the thymus gland.

15. The nervous system consists of a single subspherical ganglion (*d*), situated in the space between the inner and outer tunics, just where the anterior and lower extremity of the hypopharyngeal band joins the ventral paries. It gives off two delicate branches forward to the "languet" (16), and a great many in all directions to the parietes of the body. There were no branches traceable specially to the mouth or towards the œsophagus.

A delicate but strong vesicle attached to the anterior and lower surface of the ganglion, and containing four subhemispherical calcareous bodies, with black pigment spots on their outer surface, evidently represents the auditory vesicle and its otolithes in the gasteropod and acephalous Mollusca: and a conical depression in the outer tunic leading towards this auditory vesicle, would appear to be intended to bring it into closer relation with the surrounding medium, Plate XVI. [Plate 6] fig. 5.

16. There would appear to be yet another organ of special sense, composed of the "languet" (*f*) and the "ciliated fossa" (*w*), called by Eschricht the "längliches organ."

The "languet" (Plate XVI. [Plate 6] fig. 5) is a long tongue-shaped or conical process, fixed by its base to the ventral surface of the respiratory cavity where this is joined by the anterior extremity of the gill, and for the rest of its extent floating freely in the respiratory cavity: it is curved so as to be convex anteriorly and concave posteriorly, and its anterior surface is marked by a shallow vertical groove; at the base this groove is wider, and where it becomes continuous with the surface of the respiratory cavity, it presents a narrow median slit, which leads into a small purse-shaped cavity, flattened from side to side and richly ciliated within, Plate XVI. [Plate 6] fig. 5 *w*.

The posterior contour of this ciliated fossa is formed by a delicate thickened band or filament, much more distinct in some other species than in the present.

It would appear probable that the languet and the ciliated fossa subserve in some manner the performance of the gustatory function.

17. From each side of the base of the languet a narrow "ciliated

band" (*x*) runs upwards, until it meets with its fellow of the opposite side, the two thus encircling the anterior aperture of the respiratory cavity.

18. The dorsal wall of the respiratory cavity is marked by two longitudinal folds, running from before backwards to the mouth. These are the dorsal folds of Savigny and others; but there is an organ to which the name of "Endostyle" may be given (*c*), very distinct from these, and yet which has been invariably confounded with them, consisting of a long tubular filament, with very thick strongly refracting walls, Plate XV. [Plate 5] fig. 4 *c*. This body lies in the dorsal sinus; its anterior extremity is slightly curved downwards, somewhat pointed, and looks stronger and more developed than the posterior extremity, which is paler, more delicate and truncated. By its ventral surface this "endostyle" is attached to a ridge of the inner tunic, which rises up into the dorsal sinus.

19. It has been stated that the circulatory system consists, not of vessels with distinct parietes, but of more or less irregular sinuses. However irregular in form, the position of several of these is very constant. There is a *dorsal sinus* running along the dorsal surface and enclosing the internal shell; there is a *ventral sinus* opposite to this and containing the ganglion; there are *lateral sinuses* connecting these. Then there is the sinus in which the intestine and generative organs lie, the *peri-intestinal sinus*, and, finally, the sinus which, connecting the dorsal and ventral system of sinuses, traverses the gill and constitutes the *branchial sinus*.

These sinuses all communicate together round the œsophagus, and above and in front of this, the heart (*g*) is developed. The heart lying obliquely at the posterior extremity of the dorsal sinus, is not tubular, as it has been described; it forms not more than three-fifths of a tube; nor is it correct to say that it lies in a pericardium. Its true nature will be best conceived by supposing the inner surface of a sinus to have become developed for about three-fifths of its circumference into a free muscular membrane, Plate XV. [Plate 5] fig. 9.

This membrane is exceedingly delicate, and is composed of a single layer of flat striated muscular fibrils.

20. The direction of the circulation depends entirely upon the order of contraction of the muscular fibrils of the heart. If they contract successively from behind forwards, the blood is forced in that direction; after a certain number of such contractions, they all become simultaneously, as it were, paralysed for a short period, and then they begin to contract again, but in the inverse order, and of course with an opposite effect upon the direction of the circulation.

The blood, in its alternate flux and reflux, bathes all the internal organs—the intestine, the endostyle, the brain and the generative organs, the corpuscles finding their way as they best may among the interstices. When the force of the heart diminishes, they frequently accumulate around the intestine in consequence of becoming entangled among the meshes of the areolar tissue (13) connecting the intestine with the parietes.

21. So far, the structure of the two forms A and B has been identical; but in proceeding to examine the reproductive organs, it will be necessary to treat of each separately.

The form A is always found to possess a connected series of young forms, the so-called *Salpa* chain, encircling its visceral nucleus; the form B, on the other hand, never possesses the *Salpa* chain, but generally contains a solitary fœtus, pendent from the upper and posterior part of its respiratory cavity. It is clear therefore that in each of these forms reproduction takes place. But is the mode of reproduction in each case similar or different? Are both, processes of gemmation, or processes of sexual reproduction, or is one process of the one description, the other of the other description? To come at the solution of this question, it will be necessary to know first, the nature and relations of the chain of young in A, then the nature and relations of the solitary fœtus in B, and, finally, to trace back the development of both to their first origin.

22. *Salpa chain of* A (Plate XV. [Plate 5] fig. 1 *h*. Plate XVI. [Plate 6] fig. 1. Plate XV. [Plate 5] fig. 9). The chain is formed of a double series of fœtuses, commencing on the right side of the nucleus, curving under it, then turning upwards and over it to the right side, and finally terminating in the middle line by a free extremity midway between the two long posterior horns.

The chain is enclosed in a proper cavity, hollowed out in the substance of the outer tunic, and this sometimes opens externally opposite the free extremity of the chain, Plate XV. [Plate 5] fig. 9.

23. The fœtuses do not form a chain by mere apposition; they are all attached by pairs to one side of a cylindrical double-walled tube, which is connected, at its anterior or proximal extremity, with the system of sinuses of the parent, to the right of the heart. The tube is in fact merely a diverticulum of the sinus system, Plate XV. [Plate 5] fig. 9, and the blood contained in the sinuses passes freely into it. It is divided by a partition (*y*) into two canals, which are distinct for the whole length of the tube, except at its very extremity, where they communicate just as the two scalæ of the cochlea do; and it thence happens, that in the living animal, a constant current passes up on one

side of the partition and down on the other, the direction of the two currents being generally, but not always, reversed with the reversal of the general circulation.

If the fœtuses be traced back upon this tube, it will be found that towards the proximal end of the tube they lose their distinctive form and become mere buds, processes of its wall, Plate XV. [Plate 5] fig. 9. It may thence be conveniently termed the "gemmiferous tube."

24. The proximal extremity of the gemmiferous tube is simply transversely striated, Plate XV. [Plate 5] fig. 9 ; further on, two elevations become apparent on either side of the median line in each of these striæ. These elevations are rudiments, the inner, of the nucleus, the outer, of the ganglion of a fœtal *Salpa*. Still more towards the distal end of the tube, the young *Salpæ* are much larger in proportion to the tube ; the internal organs become marked, the heart becomes visible by its contractions, and the body itself, although the respiratory apertures are as yet only marked out, not open, contracts occasionally. Finally, the otolithes make their appearance, the body becomes larger relatively to the nucleus and ganglion, and the respiratory orifices open, Plate XVI. [Plate 6] figs. 1, 2.

25. The cavity of the gemmiferous tube communicates with the dorsal sinus system of the fœtus. Apparently the inner canal communicates by two canals, a wider and a narrower (Plate XVI. [Plate 6] fig. 1), with the anterior portion of the dorsal sinuses of the fœtus, and the outer canal communicates with the middle of the dorsal sinuses of the fœtus. However this may be, it is quite easy to watch the blood-corpuscles of the parent making their way from the gemmiferous tube into and out of the sinus system of the fœtuses. The writer has seen one of the large blood-corpuscles of the parent entangled in the heart (which was not more than $\frac{1}{500}$th of an inch long) of a very young fœtus.

It is not exactly true that *a gradual* series in the development of the fœtuses is to be traced along the gemmiferous tube. The tube is rather marked out into sharply-defined lengths (generally three in number), in each of which the fœtuses are nearly at the same stage of growth, while they are much further developed than in the "length" on the proximal side, much less advanced than in the "length" on the distal side.

26. In this species the young *Salpæ* thus produced were extruded, when fully developed, from the aperture mentioned in (22) ; but it rarely happened that even two or three adhered together, and they never formed the remarkable free-swimming chain of other species. Generally they were found solitary, presenting only on their lateral faces traces of their former adhesion. Those which were connected

adhered together in a single series, the left antero-lateral extremity of the one being applied to the right postero-lateral extremity of the other; and when they became free the traces of the connection were visible as angular processes of the sinus system.

It is not correct to say that the *Salpa* chains have organs of attachment. At first they are attached by the whole-length of their lateral faces, the sinus system of one being continuous by a wide channel with the sinus system of the other; but as they grow these communicating channels become more and more narrowed until they are mere points of connection; all communication then ceases, and the *Salpæ* become free from one another and move about independently.

27. Having thus determined the nature and relations of the *Salpa* chain, it remains only to be said, that the young when freed, have a sub-ovoid, posteriorly-pointed form, five muscular bands, facetted sides, and in short are identical in form, and ultimately in size, with the form described as *Salpa* B. One-half, therefore, of Chamisso's theory is clearly correct; *the solitary* Salpa (Salpa A) *produces the aggregate form* (Salpa B); and we may add, that this takes place by a *process of gemmation from the walls of a tube in free communication with the circulatory system of the parent.*

28. *Solitary Fœtus of Salpa* B.—Whilst this form still forms part of the chain or is but just freed, it is sure to contain a solitary fœtus; and frequently one may be found in it when it has attained its full size, but as often not.

When the solitary fœtus exists, it hangs freely in the respiratory cavity (Plate XV. [Plate 5] figs. 4, 8) by means of a pedicle attached to the upper and posterior part of its wall, on the left side of the mouth of the parent. In its youngest and most rudimentary state it is a somewhat conical papilla (Plate XV. [Plate 5] fig. 7) or bulging of the inner tunic, consisting of an inner oval or pyriform cellular mass, enveloped in a delicate transparent membrane, which appears to be a continuation of the inner tunic.

As development proceeds the inner mass becomes divided into two portions, a larger turned towards the respiratory cavity, and which projects more and more into it, and a smaller subspherical, turned towards and lying in the cavity of the sinus, and bathed by the parental blood.

29. The whole mass goes on enlarging, but the former portion faster than the latter. The former becomes somewhat ovate, with its long diameter in the same direction as the long diameter of the parent, and gradually assumes the form of a *Salpa.* The muscular bands, the gill, the ganglion and its otolithic sac become distinct, and

eventually the heart is obviously seen pulsating close behind the pedicle of attachment, Plate XVI. [Plate 6] fig. 6.

In the meanwhile the smaller subspherical mass has undergone a remarkable change. It has likewise become thrust from the sinus towards the respiratory cavity, so that it no longer lies in the former, but is situated in the thick pedicle of the young *Salpa*.

It has furthermore become hollow, and contains two perfectly distinct cavities or sacs; of these the outer is concave and cup-shaped and envelopes the inner, which is subspherical, Plate XVI. [Plate 6] fig. 6 *m*. Now the outer sac is in free communication by a narrower neck, divided into two channels by a partition, with the dorsal sinus of the fœtus; and the inner sac is in equally free communication by a neck similarly divided, with a short sinus arising immediately behind the heart; and as there is no communication between the two sacs, it follows that the current of blood in each is perfectly distinct from and independent of, that in the other. A more beautiful sight indeed can hardly be offered to the eye of the microscopic observer than the circulation in this organ. The blood-corpuscles of the parent may be readily traced entering the inner sac on one side of the partition, coursing round it, and finally re-entering the parental circulation on the other side of the partition; while the fœtal blood-corpuscles, of a different size from those of the parent, enter the outer sac, circulate round it at a different rate, and leave it to enter into the general circulation in the dorsal sinus.

More obvious still does the independence of the two circulations become when the circulation of either mother or fœtus is reversed.

30. Whether this body perform the function or not, it can hardly be wrong to give it the name of a placenta. It is identical in structure with a single villus contained in a single venous cell of the mammalian placenta, except that in the Salpian placenta the villus belongs to the parent, the cell to the fœtus; the reverse obtaining in the Mammalia.

As the young *Salpa* increases in size, the placenta, ceasing to grow, becomes proportionately smaller, until the pedicle gradually narrowing the communication with the parent ceases and the fœtus becomes free, Plate XVI. [Plate 6] fig. 3. The remains of the placenta are traceable for some time as a small diverticulum of the dorsal sinus of the young *Salpa*, Plate XVI. [Plate 6] fig. 3 *m*.

31. The latter as it grows nowise resembles its parent. It has a prismatic form, has seven muscular bands, and developes processes from its posterior extremity. It becomes indeed perfectly similar to the form which has been described as *Salpa* A.

It thence appears that the other half of Chamisso's theory is also perfectly true, viz., *the aggregate form of* Salpa (Salpa B) *produces the solitary form* (*Salpa* A), and the circulatory system of the fœtus in this case is connected with that of the parent, *not immediately, but by means of a very distinct and well-developed placenta.*

Here is one very clear distinction between the two processes of reproduction. Are there any other differences? To answer this question we must proceed to trace back both processes to their origin.

32. It has been seen that the young *Salpæ* B are developed by a process of gemmation from the gemmiferous tube of *Salpa* A. Whence comes the tube itself?

The smaller the individual of the form A examined, the shorter is the gemmiferous tube, and the less developed the buds upon it. In individuals just free, or about to be free, it is a very short cylindrical tube, arising on the right side and just in front of the heart, and curving downwards and backwards, Plate XVI. [Plate 6] figs. 3, 3 *a*.

In still smaller attached specimens it appears as a very short, somewhat conical process (imperfectly divided by a partition) of the dorsal sinus, close to the heart; its walls are smooth, and the blood-corpuscles are easily seen passing up one side and down the other of the partition, Plate XVI. [Plate 6] fig. 4.

It is clear, therefore, that the gemmiferous tube is nothing more than a stolon, containing a diverticulum of the circulatory system of the parent, and the whole process of reproduction as it is manifested in *Salpa* A is one of gemmation. *Salpa* B *is a bud of Salpa* A.

33. Following the same course of investigation with regard to the young *Salpa* A (which it has been seen is produced from *Salpa* B), it is found, that in *Salpæ* B, which are either still adherent to the gemmiferous tube or just set free, there is no protuberance of the inner tunic into the respiratory cavity; but where this afterwards exists, a pedicle of greater or less length is attached, and running backwards, carries at its extremity an oval cellular mass, Plate XVI. [Plate 6] fig. 8. This hangs suspended by its pedicle in the cavity of the sinus, and is freely bathed by the blood. In one specimen the length of the pedicle was $\frac{1}{250}$th of an inch, the long diameter of the oval body about $\frac{1}{600}$th of an inch.

In still younger forms of the *Salpa* B, and indeed as soon as the separate organs are distinguishable, the outer tunic bulges slightly in the middle line behind the outline of the posterior aperture and beneath the nucleus, Plate XVI. [Plate 6] figs. 1, 2; this protuberance is caused by the presence of a spherical body (q) about $\frac{1}{1000}$th of an inch in diameter, containing a clear vesicle $\frac{1}{1700}$th of an inch in

diameter, which again frequently contained a round opake spot or nucleus about $\frac{1}{8000}$th of an inch in diameter; the latter sometimes appeared as a thick-walled vesicle. This is plainly an ovum; a narrow pedicle (*q'*) is attached to its upper extremity and runs upwards, curving slightly forwards to the same point as in the preceding forms.

It would appear then that the *Salpa* B developes a single ovum, which is at first placed in the median line in the ventral sinus; that partly by the increase in size of the body, and partly in consequence of a shortening of its pedicle which acts as a gubernaculum, it becomes drawn from this position upwards and to the left side; and that in the meanwhile, probably in consequence of fecundation, it becomes altered in structure, and precisely similar to and identical with the cellular mass which has been seen to form the rudiment of the young *Salpa* A, Plate XVI. [Plate 6] fig. 7. In this case *the* Salpa A *would be a true embryo developed by a process of sexual generation.*

34. Sexual generation however presupposes a male fecundating organ, and this is found in *Salpa* B as a ramified body, hitherto generally called a liver (*p*), Plate XV. [Plate 5] figs. 6 and 7, closely surrounding the intestinal canal with a network, solid in the younger form, but in the older tubular, with very thin walls, and containing a vast number of pale-greenish circular cells, from $\frac{1}{5000}$th to $\frac{1}{1700}$th of an inch in diameter; and besides these detached spermatozoa, with very thin tails and long narrow heads, about $\frac{1}{1600}$th of an inch in length. The testis has no visible excretory organ, but such might well escape notice.

Nothing at all resembling this body is found in the form A; its contents sufficiently demonstrate its real nature, and its existence on the other hand is strong confirmatory evidence, if any be needed, that the pediculate body described above is a true ovum.

One curious circumstance needs to be remarked; the testis does not develope *pari passu* with the ovum and attain its full development at the same time, as might be imagined. The testis is always behind the ovum in its progress, and does not, indeed, seem to have attained its full development until the latter has become freed from the parent.

Without carefully tracing the form B through all its stages, it might readily be supposed to be always male; in fact, fully-grown specimens, while they always possess a well-developed testis, rarely contain any embryo, this being generally set free when the parent is about half or two-thirds grown. The careful observer will, however, be always able to detect a trace of its former attachment, in a sort of cicatrix, left at the corresponding part of the respiratory chamber.

35. It is not clear by what channel fecundation takes place, whether each *Salpa* B impregnates its own ovum by discharging the contents of its own testis into the circulatory fluid, which would be a procedure altogether anomalous ; or whether, on the other hand, impregnation do not rather take place from without, a presumption which is strengthened by analogy, and by the fact, that the testis does not seem to attain maturity early enough to fecundate its own ovum. The spermatic fluid may have access to the ovum by the gubernaculum becoming hollow and tubular, as will be seen to be the case in the *Pyrosomata*, and indications of such an occurrence have occasionally manifested themselves.

36. To recapitulate.—The form A (*Salpa solitaria*) produces a stolon, from which, by gemmation, arises the form B (*Salpa gregata*). This contains a testis and a single ovum attached by a pedicle or "gubernaculum" to the wall of the respiratory chamber. Fecundation takes place in a manner not yet clearly ascertained, and the "gubernaculum" shortens until the ovum is brought into close contact with the respiratory wall or inner tunic. The latter then protrudes into the respiratory canal, enveloping the ovum in a close sac ; the ovum becomes developed into an embryo, which is connected by a genuine placenta with its parent, and ultimately assuming the form of *Salpa* A becomes detached and free.

37. While Chamisso's formula, then, expressed the truth with regard to the generation of the *Salpæ*, it does not express the whole truth.

True it is, that the *Salpa solitaria* always produces the *Salpa gregata*, and the *Salpa gregata* the *Salpa solitaria* ; but it is most important to remember that the word "produce" here means something very different in the one case, from what it means in the other. In the *Salpa solitaria* the thing produced is *a bud ;* in the *Salpa gregata a true embryo.* There is no "alternation of generations," if by generation sexual generation be meant ; but there is an *alternation of true sexual generation with the altogether distinct process of gemmation.*

It would be irrelevant to discuss here the wide question of the "alternation of generations" in all its bearings ; but the writer may be permitted to express his belief, founded upon many observations upon the Polypes, Acalephæ, &c., that the phenomena classed under this name are always of the same nature as in the *Salpæ ;* that under no circumstances are two forms alternately developed by *sexual generation ;* but that wherever the so-called "alternation of generations" occurs it is *an alternation of generation with gemmation.*

38. Using the terminology of insect metamorphosis, as Chamisso

has done (70), the larva never produces the imago by sexual generation, the imago again producing the larva by sexual generation. But a pseud-imago, which is indeed nothing more, homologically, *than a highly individualized generative organ*, is developed from the larva, ova are produced by it, and from these the larva again is developed; the whole process differing from that common to animals in general, in nothing but the independence and apparent individuality of the generative organ.

39. It cannot be too carefully borne in mind that zoological individuality is very different from metaphysical individuality, and that the whole question of the propriety of the "alternation theory" as a means of colligating the facts (for at best it can be nothing more) turns upon the nature and amount of this difference.

If the true definition of the zoological individual be (as the writer believes it to be) "the sum of the phenomena successively manifested by, and proceeding from, a single ovum, whether these phenomena be invariably collocated in one point of space or distributed over many," then there is no essential difference between the reproductive processes in the higher and lower animals, and the alternation theory becomes unnecessary.

In accordance with this definition, neither the form A, nor the form B would be a zoological individual; not either of their forms, but both together, answer to the "individual" among the higher animals.

In strictness both *Salpa* B and *Salpa* A are only parts of individuals, —are organs; but as we are unaccustomed to associate so much independence and completeness of organization with a mere organ, to give them such a name would sound paradoxical. It is proposed, therefore, to call them, and all pseudo-individual forms resembling them, "zoöids," bearing in mind always that while the distinction between zoöid and individual is real, and founded upon the surest zoological basis,—a fact of development,—that between zoöid and organ is purely conventional, and established for the sake of convenience merely.[1]

40. In the *Salpæ*, then, the parent and the offspring are not dissimilar, but the individual is composed of two zoöids.

In *Cyanea*, the individual is composed of two "zoöids," a medusiform and a polypiform zoöid.

[1] For a further consideration of this subject the author begs to refer to Dr. Carpenter's "Principles of Physiology," in which the whole question of individuality in plants and animals is treated in a very clear and masterly manner; to Mr. Thwaites's papers in the Annals of Natural History; and to an attempt to apply the principles advocated in the text to the metamorphosis of the Echinoderms in a Report by himself.—*Annals*, July 1851.

In the *Trematoda* there are frequently three "zoöid" forms to the individual.

In the Aphidæ the sum of from nine to eleven "zoöids" composes the individual, the great number of zoöid forms in this case being simply an instance of that "irrelative repetition" of parts so common among the lower animals.

A similar irrelative repetition exists among the so-called "compound" animals, the Polypes and compound Ascidians; and consistently with the present theory we must call a *Sertularia* or a *Pyrosoma*, for instance, not an aggregation of individuals into a common mass, but an individual which is developed into a greater or less number of zoöid forms, which in the present case remain united.

Thus the stem and branches of the polypidom in *Sertularia* are "organs," the ovarian vesicles are "organs," the polypes are "zoöids;" the sum of the organs and zoöids constitutes the individual.

If the separate polypes be individuals, what is the polypidom which exists before them, and therefore cannot be derived from them?

It seems startling to assert that a *Salpa* of the form A with some fifty or sixty of the form B which proceed from it, constitutes but one zoological individual; still more to aver this of some millions of Aphides all proceeding indirectly from one ovum; but these difficulties have reference merely to our ordinary notion of individuality, and involve us in no self-contradictions and inconsistencies such as seem inherent in any other view of the case.

SECTION II.—*The Anatomy of* Pyrosoma.

41. This genus, first established and very imperfectly described by Peron,[1] received elaborate investigation from Lesueur[2] and from Savigny,[3] who very carefully described every part of its organization with the exception of the generative organs, and one or two other points of minor importance.

Subsequently M. Milne-Edwards[4] showed that the nature of the circulation was the same in it as in the other Ascidians.

Of the three species distinguished by Lesueur the present appears most closely to resemble the *P. atlanticum*.

42. The only specimen of this remarkable animal which the writer has had an opportunity of examining in the fresh state, was procured on the night of the 15th of June 1850, in about 45°·85 S. lat. and 110°·30 W. long. The sky was clear but moonless, and the sea calm;

[1] Annales du Museum, 1804.
[2] Journal de Physique, 1815.
[3] Mem. sur les Animaux sans Vertèbres.
[4] Comptes Rendus, 1840.

and a more beautiful sight can hardly be imagined than that presented from the decks of the ship as she drifted, hour after hour, through this shoal of miniature pillars of fire gleaming out of the dark sea, with an ever-waning, ever-brightening, soft bluish light, as far as the eye could reach on every side. The *Pyrosomata* floated deep, and it was with difficulty that some were procured for examination and placed in a bucketful of sea-water. The phosphorescence was intermittent, periods of darkness alternating with periods of brilliancy. The light commenced in one spot, apparently on the body of one of the "zoöids," and gradually spread from this as a centre in all directions; then the whole was lighted up; it remained brilliant for a few seconds, and then gradually faded and died away, until the whole mass was dark again. Friction at any point induces the light at that point, and from thence the phosphorescence spreads over the whole, while the creature is quite freshly taken; afterwards, the illumination arising from friction is only local.

43. So far as could be observed the *Pyrosoma* had no power of locomotion; any such power arising from a contraction of the hollow cylinder is out of the question, as its substance is cartilaginous and non-contractile. Any one who does not examine these animals quite closely may be readily deceived on this point; for the alternate fading and brightening of the phosphorescent light gives rise to the impression that the creature recedes from and approaches the eye; and viewing them from the deck of a ship only, it is difficult to imagine that they do not really move with some rapidity.[1]

44. The *Pyrosoma* may be described as a hollow cylinder, solid and hard to the touch, closed and rounded at one end, open at the other. A narrow lip projects inwards at the open extremity; it has been called a membranous diaphragm, but in the specimen examined it was certainly cartilaginous and immovable, like the rest of the animal. The thickness of the wall of the cylinder was about two-fifths of an inch; its diameter was about one inch and a half; its length was about 10 inches. The outer surface of the cylinder was covered with a multitude of small projections, and close to them opened small circular apertures. The inner surface of the cylinder was uneven but not rough, and was similarly pierced with circular apertures.

The wall of the cylinder consists of a vast number of minute

[1] My observations upon the power of locomotion of *Pyrosoma* were very imperfect, as I was anxious rather to attend to the more interesting points of structure. Certainly the cylinder does not contract as a whole, but it is very possible that the zoöids do, and so move by the reaction of the forced-out water against the closed end of the cylinder.

Ascidian "zoöids" lying perpendicular to the axis of the tube, and united together by a common cartilaginous basis; and the small circular apertures correspond respectively, the outer to the anterior aperture of the *Salpa*, the inner to the posterior aperture.

Each aperture is provided with a small dentated membranous valve, Plate XVII. [Plate 7] fig. 1.

45. In each zoöid there is at one point a ganglion (*d*), with a mass of deep red otolithes. As in *Salpa*, this must be called the ventral side; the opposite is the dorsal side, and contains (as in *Salpa*) an endostyle, Plate XVII. [Plate 7] figs. 1, 2 *c*. The ganglionic or ventral surfaces of all the polypes are turned the same way, and towards the open end of the cylinder.

By far the greater part of the space occupied by each zoöid is taken up by the respiratory cavity. This is elliptical, and compressed laterally. It is lined by the proper branchial network, hereafter to be described (*v*), and communicates freely by means of the apertures in the branchial network with the post-branchial or anal cavity, which, as before stated, opens into the interior of the cylinder.

46. The viscera lie behind the branchiæ. They consist of the digestive canal, heart, and generative organs.

The intestine (*r*, *s*, *t*) commences by a wide mouth with thick lips, at the posterior, ventral extremity of the respiratory cavity. The œsophagus (*r*) runs back, and then upwards to terminate in the wide subquadrilateral stomach (*t*). A narrow pylorus communicates with the intestine, which passes at first upwards and forwards, and then suddenly becoming bent upon itself, runs downwards and to the right side, to end in the wide flattened anus (*r*).

The œsophagus is dotted over with branched carmine pigment-cells; and similar cells are frequently seen upon the intestine just beyond the pylorus.

47. A tubular axis (*u*) arises from the stomach, and branches out on the rectum into a system of tubes as in *Salpa*; but the ramifications are less numerous and less regular, with wider meshes than in the latter. The tubes are less transparent and have more the appearance of solid fibres, and finally they terminate towards the anus in wide globular cæca.

The stem of this system is about $\frac{1}{1200}$th of an inch in diameter.

48. Each zoöid is composed of two tunics, an outer (α), confluent with the general cartilaginous basis, and an inner (β) continuous with the outer at its anterior and posterior extremities, and adherent to it antero-laterally, in two oval spots, one on each side, which, when examined by the microscope, appeared to consist of nothing more

than an aggregation of clear circular cells about $\frac{1}{800}$th of an inch in diameter (δ). These were considered by Savigny to be the ovaria, but they have not the appropriate structure, and it will be seen that the ova are formed elsewhere.

In all the rest of their extent the inner and outer tunics are separated by a very obvious space. This is one large vascular sinus, and the viscera lie in it and are bathed by the blood which fills it.

The heart (g) is placed on the dorsal side just behind the posterior extremity of the internal shell. In structure it perfectly resembles that of *Salpa*, and its contractions are reversed in a similar manner. No distinct vessels were to be traced in these animals.

49. The endostyle (c) resembles that of *Salpa* in its structure. It is as long as the branchial chamber, and lies in the dorsal sinus, supported by a projecting ridge of the inner tunic. On each side of it below, there is a longitudinal thickening, which readily gives rise to the appearance of four dorsal bands or "undulated vessels," described by Savigny.

50. The branchiæ (v) are symmetrical, one on each side, and are composed of a network formed by longitudinal and vertical bars or laminæ.

The vertical bars are outside; the longitudinal bars are at equal distances along their inner surface, and are attached at the point of intersection.

The vertical bars are attached to the inner tunic at their upper and lower extremities; for the rest of their extent they are free.

The longitudinal bars (v, fig. 3) are rather laminæ, flattened horizontally, slightly thickened at their free edges, and beset along the upper surface of these edges with small teeth; they project anteriorly and posteriorly beyond the vertical bars.

Both systems of bars appeared to be tubular, although no corpuscles were seen moving in them, and the edges of the vertical sinus were thickly covered with long cilia, moving in opposite directions on the opposite sides.

51. The dorsal edges of the two branchiæ were separated by a space containing the thickened dorsal folds already mentioned, and this is continuous posteriorly with a band which connects the mouth with the dorsal surface of the respiratory cavity, and allows the water to pass back on each side of it to the post-branchial cavity.

52. Anteriorly on the ventral side is an organ (fig. 10 w) analogous to the "ciliated fossa" of the *Salpæ*, and behind this a series of tongue-shaped eminences (fig. 1 f) projects into the respiratory cavity, analogous to the "languet" of the *Salpæ*.

The "ciliated fossa" is compressed laterally, and placed upon the upper surface of a protuberance, formed by the ventral wall of the respiratory cavity in the middle line. On each side a flattened ciliated band (fig. 10 *x*) runs up on the respiratory wall in front of the anterior edge of the branchiæ, and meets above with its fellow of the opposite side.

The "languets" are altogether eight in number. They extend in a longitudinal series between the ciliated fossa and the mouth. They are all slightly excavated and ciliated anteriorly.

53. Immediately beneath the ciliated fossa, and in the midst of the ventral sinus, lies the ganglion. This is about $\frac{1}{140}$th of an inch long, somewhat egg-shaped, with its large end forwards. Its posterior extremity is in contact with a mass of deep red otolithes, fig. 10 *d*.

A small nerve runs from the ganglion to the lateral ciliated band. Five or six branches are distributed to the anterior aperture, and two principal branches run backwards to the posterior aperture, giving off branches to the mouth in their course.

54. The *Pyrosomata* are hermaphrodite.

The testis (*p*) is the so-called "hepatic organ" of Lesueur, Savigny and Peron. It consists of ten, twelve, or more cæca, connected by their posterior extremities, and here joining a central duct, which opens by a papilla at the upper and posterior part of the respiratory cavity. The spermatic sacs lie loosely in a dilatation of the vascular sinus, and are bathed freely by the blood.

Each sac is delicate and thin-walled, about $\frac{1}{500}$th of an inch in diameter, and very variable in length. In adult specimens the distal or anterior end of each sac is filled with a pale cellular mass. Towards the attached end this becomes darker and more distinctly granulous, and the filiform bodies of masses of spermatozoa are plainly perceived.

The spermatozoa have narrow elongated heads and very long delicate tails.

55. There cannot be said to be any ovary properly so called. But to the left, and rather in front of the testis (fig. 5), there could always be found more or less decided traces of one or more ova.

Commonly there was a single ovum (figs. 4-6), measuring about $\frac{1}{230}$th of an inch in diameter, with a clear germinal vesicle $\frac{1}{600}$th of an inch in diameter, and a vesicular thick-walled germinal spot $\frac{1}{1600}$th of an inch in diameter.

The ovum is inclosed in a strong transparent sac, continuous with a pedicle or gubernaculum (fig. 6 *q'*), which runs to the upper and posterior part of the inner tunic on the left side, and there terminates

in a papilla, like that of the vas deferens, projecting into the post-branchial cavity.

In young specimens, when the ovum is small and the yelk pale, this gubernaculum frequently appears to be solid ; but in fully-grown specimens, when the ovum has its full size, and the yelk is darker and granulous, it presents the appearance of a wide tube, especially at its upper part. And here there was frequently an appearance of dark striæ and moving granules, prompting the belief that spermatozoa had travelled thus far.

In one instance (fig. 6) the sac of the ovum was empty and the gubernaculum or duct widely distended. The appearance of spermatozoa in the duct was here very strong, fig. 5.

None of the compound ova described by Savigny were present in the specimens of *Pyrosoma* examined.

56. The young polypes described by Savigny as existing between the fully-formed ones, in all stages of development, are formed by gemmation, Plate XVII. [Plate 7] fig. 7 *q*.

A diverticulum of the dorsal sinus of the parent is formed just above the heart ; the extremity of this diverticulum thickens and enlarges, and assumes the form of a single zoöid. For a long time a vascular connection is maintained between it and the parent, by means of a duct, in which there seemed to be traces of a longitudinal partition, as in the gemmiferous tube of *Salpa*. Ultimately the connection appears to cease, and the two polypes live on independently.

It is to be remarked, that while in *Salpa* the ventral side of the young bud is first marked out, and the communication of the parent with the young is thence on the dorsal side of the fœtus, in *Pyrosoma* the dorsal side is first developed, and the communicating canal opens on the ventral side of the young.

57. The ovum or ova, for there are sometimes two or three, are perceptible very early in the young polype produced by gemmation, and are then situated in the middle line posteriorly.

58. The muscular system is best seen in a young specimen (fig. 8 *k*). Two very delicate bands encircle the inner tunic anterior to the ganglion. From the posterior extremity of the ganglion two strong bands arise, which diverge for about half the distance between the ganglion and the mouth. Here they divide into two branches, one of which continues the original direction, while the other meets its fellow just behind the mouth. The former, as it leaves the under surface to become lateral, is much increased in size, and eventually terminates at a short distance from the generative glands, forming on each side the band of which Savigny speaks as passing towards the liver.

Midway between the ganglion and the point of division, the diverging bands give off each a thin band, which runs to the lateral oval cellular masses.

SECTION III.—*The Homology of Structure of* Salpa *and* Pyrosoma, *and of these with the ordinary Ascidians.*

59. It seems to have been pretty generally admitted by naturalists, that the *Tunicata* are susceptible of division into two great classes, the Monochitonida and Dichitonida, characterized by certain differences in the structure of the branchiæ and in the degree of adhesion of the inner and outer tunics.

Of the two species whose structure has been described, *Salpa* and *Pyrosoma*, the former was placed among the Monochitonida (or "those having the inner sac adherent throughout to the outer tunic"), while the latter was reckoned among the Dichitonida (or those "whose inner sac is adherent to the outer tunic, at its two orifices, only").

Now there is an ambiguity which must be noticed here at starting, as it is one which has caused much confusion, and must, unless cleared up, cause our conception of the real structure of the Ascidians to be very indistinct. Authors speak of the greater or less adherence of the outer and inner sacs, and consider the "outer sac" of the ordinary Ascidian to be homologous with the outer tunic of the *Salpa*. The "inner sac," again, is with them homologous with the inner tunic of the *Salpa*. But it is not so; every Ascidian, as M. Milne-Edwards has clearly shown in *Clavelina*, consists of three tunics: an outer, the *test*; a middle, which is here called outer *tunic*; and an inner, the inner *tunic*. The inner tunic of the *Salpa* answers to the inner tunic of *Clavelina*, but its outer tunic answers to the test and the outer *tunic* together (90).[1]

However, with regard to the two genera in question, whatever be the nature of the two membranes of which they are composed, there is absolutely no distinction whatever to be drawn between them.

[1] This essential difference between the test and the two *tunics* of the Ascidians has its origin in the embryo. The tunics are formed by the ordinary process of development, while the test having a totally different chemical composition, is in a manner secreted round, and envelopes the whole embryo.

There seems to be a certain independence in the mode of growth of the embryo and that of the test, the former lying at first quite free in the latter; and it appears to depend entirely upon the relative rates of growth of the two whether the resulting Ascidian shall be Monochitonidous or Dichitonidous.

The test of the Ascidian composed of cellulose is every way homologous with the test of the Mollusk composed of carbonate of lime.

The inner membrane is just as much or as little adherent to the outer in *Pyrosoma* as in *Salpa.* In each case the wide sinuses between the two membranes form the sole vascular system.

60. It may be said that there is an essential difference between *Salpa* and *Pyrosoma* in the structure of the branchiæ. A little consideration, however, will show that this is merely a difference in degree.

Savigny has shown that in certain *Salpæ* there is an upper division of the "gill," an "epipharyngeal band" (to carry out the nomenclature adopted at (10)), as well as a hypopharyngeal band.

Now in the genus *Doliolum* (88)[1] this epipharyngeal band has attained a much greater development (though the mouth still remains at the upper part of the cavity), and like the hypopharyngeal band carries a number of ciliated branchial bars. These bars have a direction more or less parallel to those carried by the hypopharyngeal band, and hence there appear to be two branchiæ, an upper and a lower.[2]

But in *Pyrosoma* the mouth is on the ventral side of the animal; the epipharyngeal band, developed in proportion to the distance of the mouth from its normal position, takes a direction at right angles to the axis, and thence comes to carry the branchial bars belonging to it parallel to the axis; while the hypopharyngeal band carrying its branchial bars as before, the two sets cross and produce the branchial network.

The line between the Monochitonida and Dichitonida then can certainly not be drawn between the *Salpæ* and *Pyrosomata.*

61. The *Pyrosomata*, in the main, have the closest similarity in structure to the Botryllidæ and other compound Ascidians; but in these latter, the separation between the test and the outer tunic becomes more and more marked, until it attains its greatest amount in the Clavelinidæ, Cynthiæ, &c.

Now does this separation furnish a character of any value or importance, systematically? Surely not, for the value of a character depends upon the number of differences of which it is a mark; and this is the mark of none.

Savigny observed the close resemblance between *Botryllus* and *Pyrosoma*, which yet differ in this character.

[1] And it may be added in the genus *Anchinaia*, described in Wiegmann's Archiv for 1833, which seems to be a most interesting transition form between the *Salpæ* and *Doliolum*, if indeed it be not the young form of *Doliolum caudatum* itself.

[2] See also on the homology of the branchial organs of the *Salpæ* and ordinary *Tunicata*, M. Milne-Edwards, Sur les Ascidies composées, p. 55.

Clavelina and *Perophora* are acknowledged to be closely allied genera, and yet in the former the test and outer tunic are separated to their utmost extent; in the latter [1] they are as closely united as in any *Salpa.*

In the Cynthiæ the test and tunics are generally very distinct, but in *Cynthia ampulloides*, judging by the descriptions of Van Beneden, they are confounded together.[2]

Again, in the *Salpa vaginata* of Chamisso, the test makes its appearance as a separate structure, and the cavity in which the gemmiferous tube lies in all the *Salpæ*, and through which it makes its way to the exterior, seems to represent the normal separation of the test and tunics.

The homology of the cellulose test of the Ascidian with the calcareous test of the Mollusk has already been adverted to; and it would seem that the separation of the former from the tunic, or its confusion with it, is of as little value as a character among the *Tunicata*, as the imbedding of the shell in the mantle in *Limax* would be in separating it from *Helix*, whose shell is distinct from the mantle.

62. It would appear, indeed, that in no natural family is it less possible to draw any very broad line of demarcation among the various members than in the *Tunicata.*

Tracing them one by one, we find that all the organs of the *Salpæ* have their homologues among the other Ascidians; the various genera passing one into the other by almost imperceptible gradations.

Even the connection of the fœtus with the parent by a placenta, a feature apparently so unique in the *Salpæ*, seems to be not without its analogue in the Didemnidæ.[3]

The actual fact of a placental circulation indeed has not been observed, but it may be surmised, as M. Milne-Edwards [4] has observed the ova to be developed within a diverticulum of the vascular system of the parent.

The peculiarly formed heart, the circulation without distinct vessels, and the reversal of its direction are common to all *Tunicata.*

[1] See the very beautiful figures and descriptions of Lister in the Philosophical Transactions for 1834.

[2] Mém. de l'Acad. Roy. de Bruxelles, tome xx.

[3] The only remaining important difference of *Salpa* from its congeners consists in the *Salpa* larvæ being tailless, while, as the beautiful researches of M. Milne-Edwards have shown, the other Ascidian larvæ have tails. This exception, however, is singularly paralleled among the Amphibia. The larvæ of the ordinary Amphibia have, as is well known, deciduous tails like the ordinary Ascidians. *In the genus* Pipa, *however, which carries its young in cells upon its back, the larva is tailless.* (Leuckart, Ueber Metamorphose, &c., Siebold, and Kölliker's Zeitschrift für Wissenschaftliche Zoologie, 1851.) Such a very striking analogy needs no comment.

[4] Obs. sur les Ascidies composées, p 23.

63. In all the *Tunicata*, again, it would seem that the first bend of the intestine (whatever its subsequent course) is dorsal, *i.e.* to the side opposite the ganglion, and almost always to the right side. *Doliolum*, however, seems to be a sinistral *Tunicate*.

What has been described in the present paper as the "Tubular System" was found by Lister (Philosophical Transactions, 1834) in *Perophora*, and described by him as "transparent vessels that may be supposed lacteals."

In *Chelyosoma* there is a mass of otolithes and a fossa, seemingly analogous to the "ciliated fossa."

The "languet" of the *Salpa* has its homologues in *Pyrosoma*, *Chelyosoma* and *Clavelina*, and is represented by smaller tentacular filaments in *Cynthia*, *Diazona*, *Synoicum* and *Polyclinum*.

64. All the *Tunicata* are hermaphrodite; and from the small size of the only efferent generative duct in the Botryllidæ, it would seem that the ova make their exit in the same way as in the *Salpæ*.

All the *Tunicata* possess the power of gemmation, and the buds are always formed as in *Salpa* (though not always with the same regularity), from a diverticulum of the sinus system.

65. With regard to the "endostyle," which appears hitherto to have been strangely confounded with the dorsal folds of the inner tunic, the writer can speak positively as to its existence in the *Salpæ*, *Pyrosomata* and certain Botryllidæ. In all these species it is figured by Cuvier, Chamisso, Savigny and Milne-Edwards,[1] but not described; and as a precisely similar structure is figured by Savigny and others in the solitary Ascidians, it is not perhaps too much to assume that the endostyle exists in them also. Should such be the case, we should be furnished with a new and very remarkable distinctive character of the *Tunicata*.[2]

The "elæoblast" of the *Salpæ* appears to be represented in the solitary Ascidians by the calcareous mass in contact with the heart, described by Van Beneden in *Cynthia ampulloides*.

66. The simple epipharyngeal and hypopharyngeal bands of the *Salpa* have been traced through their first degree of complication in *Doliolum* to *Pyrosoma* and *Botryllus*, where they form a true branchial sac, differing from that of the simple Ascidians only in the number and size of its meshes.

[1] Lister, in his description of *Perophora*, *loc. cit.*, figures the endostyle and says, "along the middle of the back is a vertical compound stripe, *d* (fig. 4), that seemed to me cartilaginous."

[2] Since the above was written the author has had the satisfaction of finding both the endostyle and the ciliated sac, in a small, very transparent *Cynthia* (—— ? sp.) obtained at Felixstow, on the Suffolk coast.

On the other hand, in *Pelonaia* the hypopharyngeal band itself has disappeared. It is a *Salpa* in which the oral and cloacal orifices have approximated while the "gill" has become obliterated.[1]

In the strange form *Appendicularia* (79), the simplification is carried a step further, for there is but one orifice, the oral. The anus opens on the dorsal surface, and a long appendage is added in the same position as that of *Boltenia*, but instead of being a long pedicle of attachment, it is a free and energetically moving fin.

67. To sum up what has been said, it appears that the *Salpæ* are not, as has been generally supposed, an aberrant form of the *Tunicata*, but rather that they are connected by insensible gradations with the other forms of the group ; neither is there any circumstance in their two modes of multiplication at all at variance with what takes place in other genera of the family.

The distinction between monochitonidous and dichitonidous *Tunicata* cannot be kept up in its present sense, for the proper inner and outer tunics are equally adherent in all *Tunicata ;* and as expressing the degree of adherence of the test to the outer tunic, the distinction is of no value, systematically, as the character may vary greatly in the same or closely allied genera.

SECTION IV.—*History of our Knowledge of the* Salpæ.

68. Forskahl, the Danish naturalist, founded the genus *Salpa* upon certain animals taken in the Mediterranean. No less than eleven species are described and figured by him (and with remarkable clearness and accuracy) in his "Descriptiones Animalium," a work which he unfortunately did not live to see published, but which made its appearance in the year 1775.

The following is a definition of the genus : "Salpa corpore libero, gelatinoso, oblongo, utroque apice aperto ; intus vacuo ; intestino obliquo variat : *a*) nucleo globoso, opaco, juxta anum *b*) nucleo nullo sed linea dorsali opaco.

"Nomen mutuatum a Σάλπα, pisce a Græcis cognito et huic vermi additum ob similitudinem formæ cum tubo canoro. Animal plerumque gregarium ; mira cohærens symmetria motum corporis per systolem et diastolem, siphonica arte perficiens."

Browne,[2] who appears to have been unacquainted with Forskahl's

[1] *Chelyosoma* would appear to resemble *Pelonaia* in the absence of any distinct branchial sac ; but Eschricht's figures are not very clear.

[2] Natural History of Jamaica, 1785.

work, gave the name of *Thalia* to some *Salpæ*, which he describes and figures in the rudest manner.

Bosc seems to have been the first to suspect the identity of these two genera, a suspicion which was converted into a certainty by the researches of Cuvier, who not only disentangled the nomenclature of the genus from the confusion into which it had fallen, but gave the first accurate idea of the anatomy of the *Salpæ*, and first announced their true zoological relations.

69. Much was added piecemeal to the foundation thus laid by Cuvier, by subsequent authors. Meyen and Milne-Edwards described the nervous system, Kuhl and Von Hasselt, Eschscholtz and Milne-Edwards, announced the singular nature of the circulation. Cuvier and Chamisso hinted, and Meyen described, the placental connection of the solitary fœtus with the parent; Eschricht and Sars declared the proximate nature and mode of origin of the *Salpa* chain.

70. Chamisso again founded the theory of the "alternation of generations," using that very phrase[1] to express the peculiarities accurately observed by him in the mode of multiplication of the *Salpæ*, but the nature and existence of the sexual organs remained undetermined until Krohn and Steenstrup in 1846 discovered the male organs; subsequently Krohn made out the true ovaries also.

Finally a most accurate account (to which indeed the present memoir can be considered only as confirmatory independent testimony) of the whole course of development and reproduction of the *Salpæ* was given by Krohn in the Annales des Sciences for 1846.

71. Without undertaking the somewhat unprofitable task of giving

[1] Justice seems to have been hardly done to Chamisso as the first promulgator of the theory of the "alternation of generations." He says at p. 10, "Qua seposita (Salpâ bicorni) *alternationem generationum* legem esse ut posuimus genericum, omnibus communem speciebus, observationibus innititur;" and at p. 3, "Talis speciei metamorphosis generationibus in Salpis duabus successivis perficitur, *forma per generationes (nequaquam in prole seu individuo) mutata.* Verum enimvero qua lege proles Salparum, ut animal ab ovo, imago a larva, inter se differunt, parum elucet." And in his interesting "Reise um die Erde," Chamisso shows still more clearly his distinct conception of the theory by the remarkable phrase, "Es ist als gebäre die Raupe den Schmetterling und der Schmetterling hinwiederum die Raupe." "It is as if the Caterpillar brought forth the Butterfly, and the Butterfly the Caterpillar."

Subsequent writers seem not to have done much more in reality than bring new cases under the law here so clearly expressed, and they do not always seem to have kept so clearly in mind the modest renunciation of any claim on the part of the theory to be an *explanation* of the facts contained in the last paragraph of the former quotation.

Finally, it must not be forgotten, that though Chamisso was the first promulgator of the "alternation," he expressly (with a candour impossible to be too much commended) gives the credit of the conception to his companion Eschscholtz, "generationis Salparum primus et perspicax fuit indagator amicissimus Eschscholtz," p. 9, and again in the preface to the second fasciculus of his observations.

a detailed historical account of all that has been written upon the *Salpæ*, it may be of interest to notice, with a view to reconcile, a few of the more important discrepancies among the statements of the chief investigators. And first :

Of the sides and ends of the Salpæ.—On so simple a matter as this, almost every writer has different views. Cuvier calls the ganglionic surface ventral, the opposite dorsal, the nuclear end anterior, the opposite posterior. Savigny appears to follow him. Chamisso follows Cuvier as to the anterior and posterior ends, but reverses the dorsal and ventral sides.

MM. Quoy and Gaimard give the ganglionic end as anterior, the nuclear as posterior, the nuclear side as ventral, the ganglionic as dorsal.

Meyen gives the same determination. Eschricht considers the nuclear end to be posterior, the ganglion side ventral ; as also Sars.

M. Milne-Edwards seems to follow Chamisso. It is much to be wished that some uniform nomenclature could be adopted. The reasons for the terms used in the present paper have already been given (5).

72. *The Nervous System.*—The nervous system was denied by Cuvier altogether. Savigny describes the ganglion, without recognizing its true nature, as the " tubercule qui dans les Ascidies est contigu au gros ganglion."

Chamisso describes what appears to be the thickened edge of the " ciliated fossa," and states that Eschscholtz considered it to be a nerve (*op. cit.* p. 5).

Quoy and Gaimard describe the ganglion, but omit all mention of the auditory sac.

Meyen claims the discovery of the true nervous system ; but although he figures it pretty accurately, he omits all mention of the otolithic sac, and seems after all in doubt whether it may not be a respiratory organ ; and it was reserved for M. Milne-Edwards to give the first satisfactory account of these structures.

Both Eschricht and Sars subsequently omit to describe the auditory sac.

73. *The " Ciliated Sac" and " Languet."*—Cuvier refers to this organ in *Salpa Tilesii* as " l'anneau irregulière qui la termine (la branchie) en arrière."

It has already been mentioned that this organ is mentioned by Chamisso as a problematical nervous apparatus. Quoy and Gaimard described its thickened rib as a vessel, adding, " nous dirons un vaisseau parceque nous croyons avoir vu le sang cir-

culer dans son intérieur," apparently mistaking the ciliary motion for a circulation.

Meyen calls it the "Respirations-ring," and says that it is a respiratory organ. He first described the cilia, but denies the existence of any aperture leading into the organ.

In *S. mucronata*, not perceiving that he has to do with the very same organ under a different form, he describes the "ciliated sac" as a testis. The languet he calls simply "Haken."

Eschricht gives it and the languet together, the name of "das längliche organ," and considers it as a tactile organ analogous to the pulps of bivalves. He rightly describes the nervous cords connecting it with the ganglion.

Sars confirms Eschricht's view, and considers the organ as analogous to the tentacles of the Ascidians, which, however, cannot be the case, as in many Ascidians (e.g. *Clavelina*) the tentacles and the "languets" co-exist.[1]

M. Milne-Edwards figures the "ciliated fossa" as the "fossette prébranchiale" in the plates of the last (commemorative) edition of Cuvier's "Règne Animal."

74. *The Structure of the Heart.*—Eschricht and Sars describe the heart to be composed of a series of vesicles, which is certainly a mistake, arising from the fact that the heart always presents two or three constrictions, so as to appear almost moniliform.

75. *Tubular System.*—This is figured by MM. Quoy and Gaimard (pl. 88, fig. 12) in *Salpa pinnata*, under the name of "vaisseaux mésenteriques." Is it to this structure to which M. Krohn refers, when he says that "the meshes or lamellæ of the elæoblast are traversed by numerous vessels opening into two trunks, which apparently form the attachment between this organ and the visceral nucleus?"

Perhaps also it is to this system that Eschricht refers when he speaks of the intestine as beset with "stalked granules."

76. *The Gemmiferous Tube.*—Cuvier, Savigny, Chamisso, and Quoy and Gaimard consider this structure as more or less partaking of the nature of an ovary.

Meyen mistakes it for a liver in *Salpa democratica*. Eschricht describes the process of development of the young from the gemmiferous tube and their connection with it very carefully; but he does not seem to consider it as mere gemmation.

He calls the organ "Keim-röhre," germ-tube, and considers it as a

[1] In the *Cynthia* examined by the author (see note (65)), the "ciliated sac" was seated upon a tubercle, but there was no "languet."

"quite new form" of propagative organ. From the mode of expression in the following paragraph he evidently thinks the propagation here to be in some manner sexual. "Die Eintheilung in Strecken deren jede Fötus von einerlei Ausbildung enthält, deutet allzu bestimmt auf verschiedene Befruchtungen hin, als das hier nicht eine wiederholte Geburt in längeren Zwischenzeiten anzunehmen wäre."

Sars conjectures that the solitary fœtuses arise by a process of sexual generation, but does not state very clearly what he considers to be the nature of the production of the associated forms.

77. *The Placenta.*—Cuvier speaks of finding a fœtus attached to the parent by a pedicle ; and referring to a figure, he says : "Ce corps rond (evidently the placenta) seroit-il un organe servant uniquement pendant le temps de la gestation pour établir l'union entre la mère et son petit et qui s'effaceroit ensuite?"

Chamisso calls the pedicle of attachment "pediculus umbilicalis;" the placenta "globulus opacus."

Meyen was the first to give this structure the name of placenta, and his account of it is so very clear and precise, that it is wonderful it should have been subsequently forgotten or overlooked. He says, "Wir haben bei ganz jungen Individuen den Verlauf der Blutbewegung selbst bei 200-maliger Vergrösserung beobachten können. Der Muttertheil der Placenta hat nur wenige Gefässen um so mehr aber der Fötus-theil, in dem sich ein ausserordentliches Convolut von Gefässen befindet, das sich in einem Stämme endigt, der sich in das grosse Bauchgefäss ganz in der Nähe des Hergens ergiesst. Ein unmittelbares uebergehen der Blutgefässe ausdem Mutter-theil in dem Fötus-theil haben wir nicht sehen können. Hat der Fötus die hinlängliche Ausbildung im Leibe der Mutter erreicht, so verwächst das grosse Blut-gefäss und die Placenta fällt ab."—P. 400.

78. After what has been stated concerning the development of the two forms of the *Salpæ*, it would be useless to enter upon the consideration of the various theories propounded since the time of Chamisso (such as that of Eschricht for instance) to account for the phenomena they present.

It may be sufficient to say, that it is now quite certain that the *Salpæ* never unite after being once separated, and that they do not produce successive broods of a different form.

Much remains to be done with regard to the minute process of development of the young forms of both kinds, and to this difficult inquiry it is to be hoped that future observers will address themselves.[1]

[1] An essential service to zoology will be rendered by any one who will revise and critically compare the species of the *Salpæ*. At present, they are in a most unedifying state of hopeless confusion.

In order to avoid the necessity of incessant references to the text, a list of the works consulted and alluded to, is here subjoined in chronological order.

SALPA.—Forskahl. Descriptiones Animalium, 1775.
Browne. Natural History of Jamaica, 1785.
Cuvier. Mémoires du Museum, 1804.
Savigny. Mémoires sur les Animaux sans Vertèbres, 1816.
Quoy and Gaimard. Freycinet's Voyage, 1817-20.
Chamisso. De Animalibus quibusdam e classe Vermium Linnæana. Fasc. i. 1819.
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Kuhl and Von Hasselt. Annales des Sciences Naturelles, t. iii. 1824.
Eschscholtz. Isis, 1824.
Quoy and Gaimard. D'Urville's Voyage, 1826-29.
Meyen. Beiträge zur Zoologie, Nova Acta Nat. Cur. t. xvi. 1832.
Milne-Edwards. Annales des Sciences Naturelles, 1840.
Krohn. Ueber die Mannlichen Zeugungs Organe der Ascidien u. Salpen, Froriep's Notizen, 1841.
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Sars. Fauna Littoralis Norvegiæ, 1846.
Steenstrup. Ueber das Vorkommen d'Hermaphrodismus, 1846.
Krohn. Annales des Sciences Naturelles, 1846.

THE ASCIDIANS IN GENERAL.—Lister. Philosophical Transactions, 1834.
Milne-Edwards. Sur les Ascidies composées, 1841.
Van Beneden. Mémoires de l'Académie Royale de Bruxelles, t. xx.
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Rupert Jones. Art. *Tunicata*, Cyclopædia of Anatomy and Physiology.

PYROSOMA.—Peron. Annales du Museum, 1804.
Lesueur. Journal de Physique, 1815.
Savigny. *Op. cit.*
Milne-Edwards. Comptes Rendus, 1840.
Milne-Edwards. Annales des Sciences, t. xiii.

[The explanation of the three plates accompanying this paper is given at the end of the next following paper, which was published with it in the *Phil. Trans.* for 1851.—EDS.]

VIII

REMARKS UPON APPENDICULARIA AND DOLIOLUM, TWO GENERA OF THE TUNICATA

Philosophical Transactions of the Royal Society, 1851, *pt. ii. pp.* 595–606

79. THE genus *Appendicularia* was first formed by Chamisso from an animal found by him near Behring's Straits, and thus described: "Corpus gelatinosum, subovoideum, vix quartam pollicis partem æquans, punctis rubescentibus (interaneis) transparentibus. Appendix gelatinosa cestoidea, rubro marginata corpore duplo vel triplo longior. Motu flexuoso natationi inserviens. Motus animalis vividus." And he adds, "genus ultra recognoscendum, generi Cestum (Les.) forsitan affine." The specific name "flagellum" was conferred upon the animal, and it was figured (P. XXXI.), though very indifferently.[1]

Ten years afterwards (in 1828) Mertens, voyaging in the same regions, rediscovered this animal, and he subsequently published a long account of it[2] under the name of *Oikopleura Chamissonis.*

The only other notice of the genus (so far as I am aware) is that given by MM. Quoy and Gaimard.[3] It was observed in immense masses off Algoa Bay, South Africa, and was called by them *Fritillaria*, until they afterwards became acquainted with the descriptions of Chamisso and Mertens. Recognising as they do the priority of discovery of the former, they yet adopt the name conferred by the latter, and, without any very just reason, give to the specimens observed by themselves a new specific name, *O. bifurcata.*

Vast numbers of the species observed by myself were found on the coast of New Guinea and in the Southern Pacific. The differences

[1] De Animalibus quibusdam e classe Vermium, Fasc. Secundus. Nova Acta Acad. Cur. tom. x. 1821.

[2] In the Mémoires de l'Acad. Imp. de St. Pétersbourg 1831.

[3] Zoology of the Astrolabe, vol. iv. p. 304.

separating this from the species observed by Mertens are not to my mind sufficient to form the basis of any specific distinction, and as the description given by MM. Quoy and Gaimard, and by Chamisso, are too imperfect to establish any certain distinguishing characters in their case either, I shall consider that only one species has been observed. And as I can see no reason for the construction of a new and by no means euphonious name by Mertens, I shall retain both the generic and specific names given by Chamisso, *Appendicularia flagellum* (Chamisso), Syn. *Oikopleura Chamissonis* (Mertens), *Oikopleura bifurcata* (Quoy and Gaimard).

80. The animal has an ovoid or flask-like body, Plate XVIII. [Plate 8] fig. 1, one-sixth to one-fourth of an inch in length, to which is attached a long curved lanceolate appendage or tail, by whose powerful vibratory motions it is rapidly propelled through the water.

The body frequently appears wrinkled and crumpled externally, and its upper, smaller extremity has rarely clear and well-defined edges. The lower part of the body is frequently separated from the upper by a slight cleft or constriction, fig. 4, and it is here that Mertens places the orifice of the mouth, supposing indeed that the upper part of the body plays the part of a maxilla !

81. The smaller extremity of the animal is perforated by a wide aperture (*d*) which leads into a chamber, which occupies the greater part of the body, and at the bottom of this chamber is the mouth. The chamber answers to the respiratory cavity of the *Tunicata*, and is lined by an inner tunic distinct from the outer ; the space between these, as in the *Salpæ*, being occupied by the sinus system.

On the side to which the caudal appendage is attached, an endostyle (*c*), altogether similar to that of the *Salpæ*, lies between the inner and outer tunics ; and opposite to this, or on the ventral side, close to the respiratory aperture, there is a nervous ganglion, to which is attached a very distinct spherical auditory sac, containing a single, also spherical, otolithe. The sac is about $\frac{1}{200}$th of an inch in diameter. The otolithe about $\frac{1}{800}$th, figs. 1, 2, 4 *a*.

Anteriorly, a nerve is given off from the ganglion (*a*) which becomes los about the parietes of the respiratory aperture ; another large trunk passes backwards (*b*) over the left side of the œsophagus, and between the lobes of the stomach, until it reaches the appendage, along the axis of which it runs, giving off filaments in its course, fig. 2. I did not observe anything resembling the "languet" of the *Salpæ* ; but Mertens describes two leaf-like laminæ existing, one on each side of a "semicylindrical" body, which seems to be the nervous ganglion.

82. There is no proper branchia ; but that organ seems to be repre-

sented by a richly ciliated band or fold (*e*) of the inner tunic, which extends from the opening of the mouth forwards, along the ventral surface of the respiratory cavity, to nearly as far as the ganglion ; when it divides into two branches, one of which passes up on each side, so as to encircle the cavity (*f*). This circlet evidently represents the "ciliated band" of *Salpa*.

The mouth (*g*) is wide, and situated at the posterior part of the ventral paries of the respiratory chamber. The œsophagus (*h*) short, and slightly curved, opens into a wide stomach (*i*) curved transversely, so as to present two lobes posteriorly.

Between the two lobes, posteriorly, the intestine (*k*) commences, and passing upwards (or forwards) terminates on the dorsal surface just in front of the insertion of the caudal appendage (*l*).

The heart lies behind, between the lobes of the stomach. I saw no corpuscles, and the incessant jerking motion of the attached end of the caudal appendage rendered it very difficult to make quite sure even of the heart's existence.

83. Mertens describes a vascular system, consisting of an aortic vessel, which runs forwards on the dorsal surface, and of a principal vein of a red colour, which passes to the ventral surface, and there divides into three branches, one of which runs forwards to the "semicylindrical body" (ganglion ?), and the other two pass to the dorsal region.

A circular canal communicating with the aortic vessel exists, he says, on each side of the anus, and is connected with the ventral vessel by means of a vessel, through which no corpuscles were seen to pass.

I have seen nothing of this vascular system. The caudal appendage (A) is attached or rather inserted into the body on the dorsal surface just behind the anus. It consists of a long, apparently structureless, transparent, central axis (*m*), rounded at the attached, and pointed at the free end. This axis is enveloped in a layer (*o*) of longitudinal, striped, muscular fibres ; which form the chief substance, in addition to a layer of polygonal epithelium cells, of the broad alary expansion on each side of the axis.

I did not observe the lateral canal containing air, described by Mertens.

84. The only unequivocal generative organ I found in *Appendicularia* was a testis (*p*), consisting of a mass of cells developed behind and below the stomach, enlarging so much in full-grown specimens as to press this completely out of place.

In young specimens the testis is greenish, and contains nothing but small pale circular cells ; but in adults it assumes a deep orange-

red colour, caused by presence of multitudes of spermatozoa, whose development from the circular cells may be readily traced.

This orange-red mass, or rather masses, for there are two in juxtaposition, is described by Mertens as the "Samen-behälter" or vesiculæ seminales. He describes them as making their exit, bodily, from the animal, and then becoming diffused in the surrounding water. This circumstance, indeed, appears to have furnished his principal reason for believing these bodies to be what the name indicates.

The spermatozoa have elongated and pointed heads about $\frac{1}{5000}$th of an inch in length, and excessively long and delicate filiform tails.

Mertens describes as an ovary, two granulous masses, which he says lie close to the vesiculæ seminales, and have two ducts, which unite and open into this "ovisac."

This appears to me to be nothing more than the granulous greenish mass of cells and undeveloped spermatozoa, which exists in the testis at the same time as the orange-red mass of fully developed spermatozoa. I saw nothing of any ducts, nor do I know what the "ovisac" can be, unless it be a further development of an organ which I found in two specimens (fig. 3 *q*), consisting of two oval finely granulous masses, about $\frac{1}{300}$th of an inch in diameter, attached, one on each side of the middle line, to the dorsal parietes of the respiratory cavity, and projecting freely into it.

Mertens' "ovisac" has about the same position as these bodies, and he says he saw "living animals" proceed from it, the part being afterwards evidently collapsed.

Unfortunately, however, he does not appear to have noticed the endostyle, whence confusion might readily arise; nor does he give the slightest hint as to the nature of the "living animals" which he saw come forth.

85. Still less am I able to give any explanation of the extraordinary envelope or "House" to which, according to Mertens, each *Appendicularia* is attached in its normal condition. I have seen many hundred specimens of this animal, and have never observed any trace of this structure; and I have had them in vessels for some hours, but this organ has never been developed, although Mertens assures us that it is frequently re-formed, after being lost, in half an hour.

At the same time it is quite impossible to imagine, that an account so elaborate and detailed, can be otherwise than fundamentally true, and therefore, as Mertens' paper is not very accessible, I will add his account of the matter, trusting that further researches may clear up the point.

The formation of the envelope or "Haus" commences by the

development of a lamina from the "semicylindrical organ" (ganglion ?). This, as it grows, protrudes through the opening at the apex of the animal (respiratory aperture). Its corners then become bent backwards and inwards, and thus a sort of horn is formed on each side, the small end of which is turned towards the apex of the animal, while its mouth looks backwards, downwards and outwards.

At the same time two other horns are developed upwards (the animal is supposed to have its small end downwards), one on each side. These are smaller and more convoluted than the others.

This four-horned structure consists of a very regular network of vessels, in which, at the time of the development of the organ, a very evident circulation is visible ; the blood-corpuscles streaming from the attached end of the organ. " The clearness with which the circulation was perceptible, together with the great abundance of vessels and the large extent over which they were spread, were circumstances which led me (says Mertens) to believe this truly enigmatical structure to be an organ, whose function was the decarbonization of the blood. The ease with which the animal becomes separated from this organ is no objection to this view ; the necessity there seems to exist for the reproduction of the latter rather confirming my opinion."

It is highly desirable that more information should be gained about this extraordinary respiratory organ, which, if it exist, will not only be quite *sui generis* in its class, but in all animated nature. And in a physiological point of view, the development of a vascular network, many times larger than the animal from which it proceeds, in the course of half an hour, will be a fact equally unique and startling.

86. As to the zoological relations of *Appendicularia*, its discoverer, as we have seen, considers that " it may possibly be allied to *Cestum*," a conjecture in which no one can possibly coincide.

Mertens, on the other hand, says, " The relation of this animal with the *Pteropoda* is unmistakeable ; if the *Oikopleura* possessed two tail-like appendages, every one would recognize in them the wings of the *Pteropoda* ;" and he proceeds to draw, what seems to me, a very forced comparison between *Oikopleura* and *Clio*.

I do not think that any one who has read the preceding pages will be at all disposed to agree with Mertens either.

87. For my own part, I think there can be no doubt that the animal is one of the *Tunicata*. The whole organization of the creature, its wide respiratory sac, its nervous system, its endostyle, all lead to this view.

In two circumstances, however, it differs widely from all *Tunicata* hitherto known. The first of them is, that there is only one aperture,

the respiratory, the anus opening on the dorsum; and secondly, that there is a long caudal appendage.

As to the first difference, it may be observed, that, in the genus *Pelonaia*, an undoubted Ascidian, there are indeed two apertures, but there is no separation into respiratory and cloacal chambers. Suppose that in *Pelonaia* the cloacal aperture ceased to exist, and that the rectum, instead of bending down to the ventral side of the animal, continued in its first direction and opened externally, we should have such an arrangement as exists in *Appendicularia*.

With regard to the second difference, I would remark, that it is just the existence of this caudal appendage which makes this form so exceedingly interesting.

It has been long known that all the Ascidians commence their existence as larvæ, swimming freely by the aid of a long caudate appendage; and as in all great natural groups some forms are found which typify, in their adult condition, the larval state of the higher forms of the group, so does *Appendicularia* typify, in its adult form, the larval state of the Ascidians.

Appendicularia, then, may be considered to be the lowest form of the *Tunicata*; connected, on the one hand, with the *Salpæ*, and on the other with *Pelonaia*, it forms another member of the hypothetical group so remarkably and prophetically indicated by Mr. MacLeay, and serves to complete the circle of the *Tunicata*.

88. *Doliolum.*—This name was given by Otto [1] to a free-swimming gelatinous case, altogether structureless, of which a single example was found by him in the Gulf of Naples. Its nature is altogether unknown, for it is hardly justifiable, in the face of Otto's words, "Die Ränder sind aber völlig glatt ohne alle Spur von Zerreissung, nirgend sieht man inwendig Rauhigkeiten wo die Eingeweide angessessen haben könnten und die äussere Haut geht ohne Unterbrechung in die innere über," to assume with MM. Quoy and Gaimard, that it is only a *Biphore* whose intestines have been destroyed by a parasitic *Phronima*.

Furthermore Otto states that the animal moved by a "worm-like contraction of its walls," which by no means describes the mode of contraction of the *Salpæ*, with which animals he was perfectly acquainted, and with a mutilated specimen of which, he expressly states he might, except for its peculiar motion, have confounded the form he describes.[2]

[1] Nova Acta Acad. Curiosorum t. xi. pars secunda, pp. 313 and 314.

[2] Prof. E. Forbes informs me that a body answering precisely to Otto's description, was found by him, occurring in considerable numbers, on the coast of Scotland, and was eventually discovered to be nothing more than the detached siphonic tubes of *Solenocurtis strigillatus*.

MM. Quoy and Gaimard,[1] altogether denying the existence of Otto's genus as a distinct form, appropriated his name for two species of tunicate animals observed by them at Amboyna and Vanikoro, and which they justly recognized as being very closely allied to the *Salpæ*.

Of these two species, *Doliolum denticulatum* and *Doliolum caudatum*,[2] the former is the only one with which I have met.

MM. Quoy and Gaimard give only the following short description :—

" Its form is nearly that of the vessel from which we have derived its generic name, that is to say, it is enlarged in the middle and narrowed at its two extremities where the openings are situated. The anterior opening is somewhat projecting and denticulated like a crown. Eight circles in relief surround the body at nearly equal distances. They have rather a polygonal than a circular form, and are probably vessels. In the interior the branchia is visible, divided into two portions, which have their oblique lamellæ upon a central vessel, as in the Pectinibranchiata. Near the union of the two divisions posteriorly is the heart, and between them (?) a vessel, the aorta, ascends ; not far from the heart is a transparent nucleus. This is all that the vivacity of the mollusk, which bounded like an arrow through the water, allowed us to make out of its organization."

Although I cannot think that MM. Quoy and Gaimard have done well in appropriating Otto's name to an animal confessedly different from that which he describes, it will perhaps cause least confusion to follow their example.

The specimens which I examined were taken in the South Pacific, a little to the northward of Sydney, N.S.W., between Sydney and New Zealand, and in considerable numbers just at the entrance of the Bay of Islands.

89. *Doliolum denticulatum*, figs. 5, 6.—A small transparent body, varying in length from one-sixth to one-third of an inch, and looking very much like a barrel open at each end, which swims by contracting its whole body, and forcing the water out at one or the other extremity.

The apertures are considerably less in diameter than the central cavity. The anterior (*d*) is produced into a sort of tube, with about twelve rounded dentations, which are turned inwards. The base of the tube is surrounded by a thickened muscular rim.

[1] Voyage de l'Astrolabe. Zoologie, t. iii. part 2, p. 599.

[2] Little more than a description of the outward form is given by MM. Quoy and Gaimard of the *Doliolum caudatum*, but it strikingly agrees in everything with what one of the associated forms of the singular genus *Anchinaia* might be supposed to become if set free ; unfortunately, the description of the latter genus itself is very scanty. See note (60).

Has the *Doliolum denticulatum* itself been ever an attached form ? From certain appearances (90) this appears very possible.

The posterior extremity is similarly produced into a short tube with a thickened base, but the tube looks outwards, and its walls are very delicate, and consist of fine fibres like those of the fin of *Sagitta*.

90. The body of the animal consists of two tunics, an inner and an outer,[1] which surround a wide central respiratory cavity.

Six muscular bands (*t*), pretty nearly equidistant, gird the inner tunic.

In some specimens a sort of shrivelled tubular process projects on the dorsal surface posteriorly between the two last muscular bands. Is this the remains of an earlier pedicle of attachment?

91. A tubular endostyle (*c*) lies in the dorsal sinus between the first and third muscular bands.

In the ventral sinus a round ganglion (*a*) lies just in front of the third muscular band. It gives off several long nerves, four of which are especially remarkable, and run diagonally to the anterior and posterior apertures. There is no auditory sac nor otolithes.

92. The branchiæ divide the respiratory cavity into an anterior and a posterior chamber. They are formed by the epipharyngeal and hypopharyngeal (*x*) bands which stretch across the respiratory cavity, supporting on each side a number of tubular bars (*y*). In the upper and lower division of the branchiæ, these bars are adherent to the walls of the respiratory cavity, *i.e.* to the inner tunic, and there their canals open into the lateral sinuses; but in the middle part of the branchiæ their extremities unite and form loops without adhering to the inner tunic, merely lying against it. There is a free passage for the water between the bars, and on each side of the central supporting bands.

The edges of the bars are richly ciliated, and the cilia of their opposite sides move in opposite directions.

Although it appeared quite certain that the canals of the bars communicated with the sinus system, yet no blood-corpuscles could be traced into them.

The branchial bars did not extend so far forward above as below. In the former case they reach as far as the second muscular band only, in the latter, beyond the first; seen from above or below, the branchia appeared as an oval plate, with a clear space down its middle and transverse bars on each side.

93. The mouth (*g*) opens in the middle of the upper division of the

[1] The outer tunic, which I consider as homologous with the test and outer tunic of the Ascidian fused together, was found by MM. Löwig and Kölliker to contain cellulose, whence they concluded the Ascidian nature of the animal, a deduction strikingly confirmed by anatomical investigation.

gill, just anterior to the fourth muscular band ; a narrow œsophagus (*h*) leads from it into a two-lobed stomach (*i*) ; from this a narrow intestine passes, and bending a little upwards and then downwards and to the left side, terminates in a papillary (*l*) anus. Just at its bend the intestine gives attachment to three or four small cæca (*s*) which appear to represent a liver, and a system of transparent anastomosing tubules, similar to that described in *Salpa*, arises from the stomach and envelopes the intestine in a network.

The heart (*r*) lies above and in front of the mouth. In structure it resembles that of *Salpa*. There are no vessels of any kind, the blood-corpuscles making their way at random among the viscera. No reversal of the circulation was observed in this Ascidian.

94. All the specimens examined possessed only the male generative apparatus, in the shape of a long tubular[1] testis (*p*), placed on the right side and below, and opening posteriorly into the respiratory chamber by a papillary elevation (*p′*) just before the penultimate muscular band.

The testis lies quite freely in the sinus, and is bathed by the blood (fig. 7).

When most fully developed the testis nearly equals the body in length ; but in young specimens it may be not more than one-half to one-third that size.

The young testis is a delicate sac, containing a mass of circular cells, about $\frac{1}{3300}$th of an inch in diameter, of a pale greenish colour, and flattened.

As development proceeds, these cells assume a redder tint, and become perfect spermatozoa with elongated cylindrical heads $\frac{1}{2500}$th of an inch in length, and very delicate, long filiform tails.

95. There is a small cavity (*u*) resembling the ciliated fossa of the *Salpæ*, seated upon the anterior face of the singular process of the ventral paries of the respiratory cavity.

This process lies anterior to the first muscular band ; it is somewhat conical and excavated behind. The two lips of the excavation are thickened and ciliated, and the right lip is continuous on the left side with a ciliated band, which runs up parallel with the first muscular band, passes over to the right side, and running down, becomes eventually lost in the right portion of the base of the conical process.

This would seem to be a rudimentary languet. A number of small granular masses were always to be seen attached to the inner tunic close to the posterior aperture.

The structure of the branchiæ of this Ascidian, the position of the

[1] Very similar to that of *Salpa cristata*, described as an hepatic organ by Meyen.

two orifices, and the structure of the testis, all indicate a position for *Doliolum* intermediate between *Salpa* and *Pyrosoma.*

Its apparent unisexuality very likely arises from the ova being developed, and leaving the parent in a younger state than any I examined. I have elsewhere mentioned the liability to deception in *Salpa* from a similar cause.

Note.—Since writing the above I have found a short notice of *Appendicularia* in Müller's Archiv for 1846,[1] under the name of *Vexillaria flabellum.* The describer, Prof. Müller, confesses that he does not know in what division of the animal kingdom to place this creature; and his account of its structure is not a little vague, including little more than its mere external appearance. He does not seem to have observed anything corresponding to the "Haus" of Otto.

DESCRIPTION OF THE PLATES.

Pl. XV. [Plate 5] Salpa.

Fig. 1. *Salpa* A.
Fig. 2. *Salpa* B.
Fig. 3. Dorsal view of *Salpa* A, the muscular bands being omitted.
Fig. 4. Dorsal view of *Salpa* B, the muscular bands being omitted.
Fig. 5. Intestinal canal of *Salpa* A.
Fig. 6. Intestinal canal of *Salpa* B.
Fig. 7. Dorsal view of extremity of *Salpa* B.
Fig. 8. Part of the respiratory chamber of *Salpa* B, showing the fœtus suspended. View from above.
Fig. 9. Connection of the gemmiferous tube with the heart.

Pl. XVI. [Plate 6] Salpa.

Fig. 1. Young gemmæ (*Salpa* B) attached to the gemmiferous tube.
Fig. 2. Nuclear end of one of these, showing the ovum and its pedicle or gubernaculum.
Fig. 3. Nuclear end of a very young *Salpa* A, just detached.
Fig. 3[a]. Placenta and gemmiferous tube of this enlarged.
Fig. 4. Heart, placenta, and gemmiferous tube of a young *Salpa* A, showing the rudimentary condition of the last structure.
Fig. 5. Ganglion, otolithic sac, and languet.
Fig. 6. Young *Salpa* A, still attached by its placenta in the interior of *Salpa* B

Pl. XVII. [Plate 7] Pyrosoma.

Fig. 1. A single "zoöid," viewed from the right side.
Fig. 2. A single "zoöid," viewed from above.
Fig. 3. Part of the branchial network.
Fig. 4. The ovum with its pedicle *in situ.*
Fig. 5. Testis and ovisac *in situ,* both emptied of their contents.
Fig. 6. Ovum and pedicle.
Fig. 7. A young zoöid developed by gemmation.

[1] Bericht über einige neue Thierformen der Nordsee.

Fig. 2.

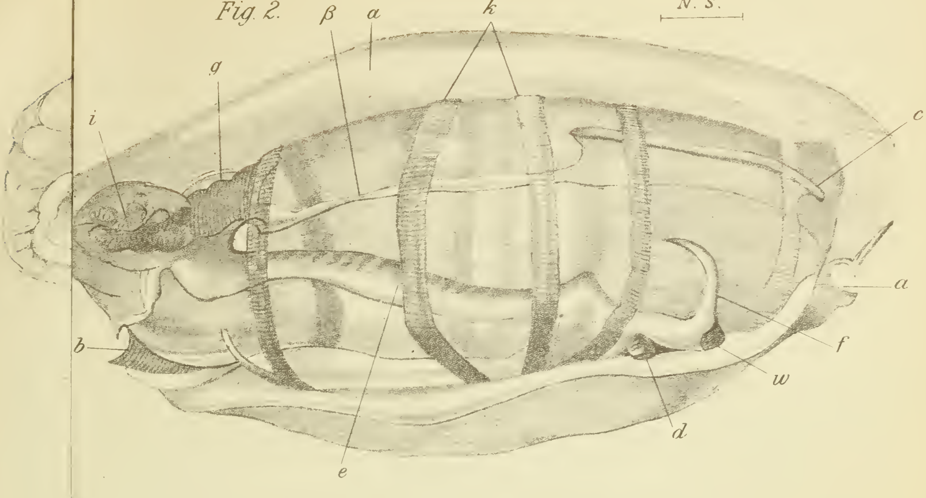


Fig. 3.

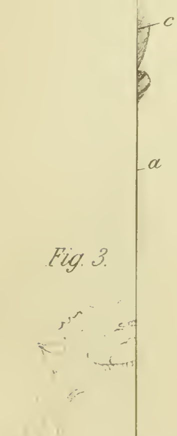


Fig. 4.

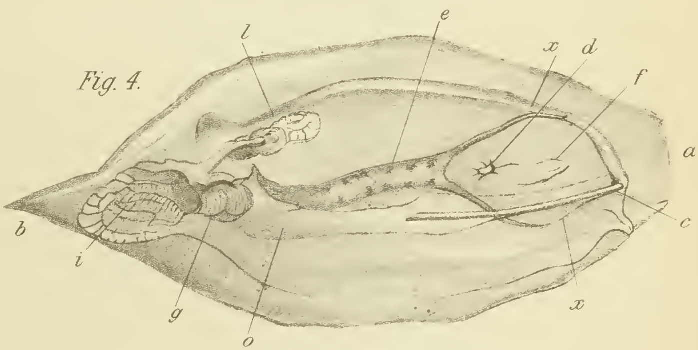


Fig. 7.

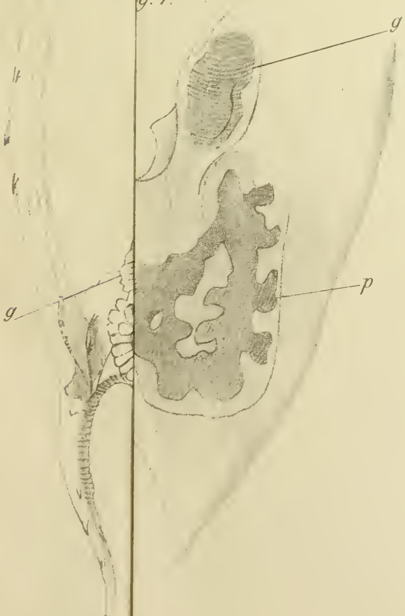
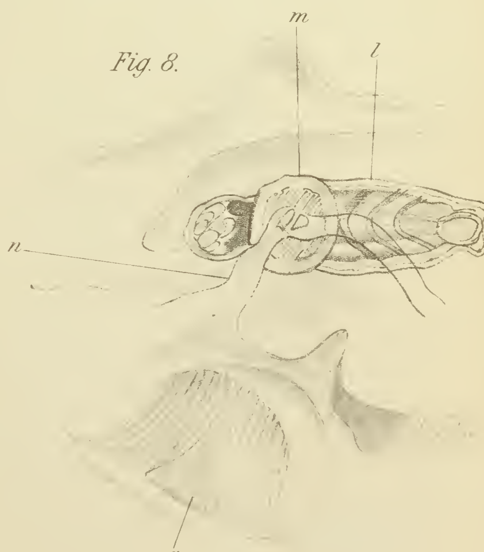


Fig. 8.



Ad. nat. d

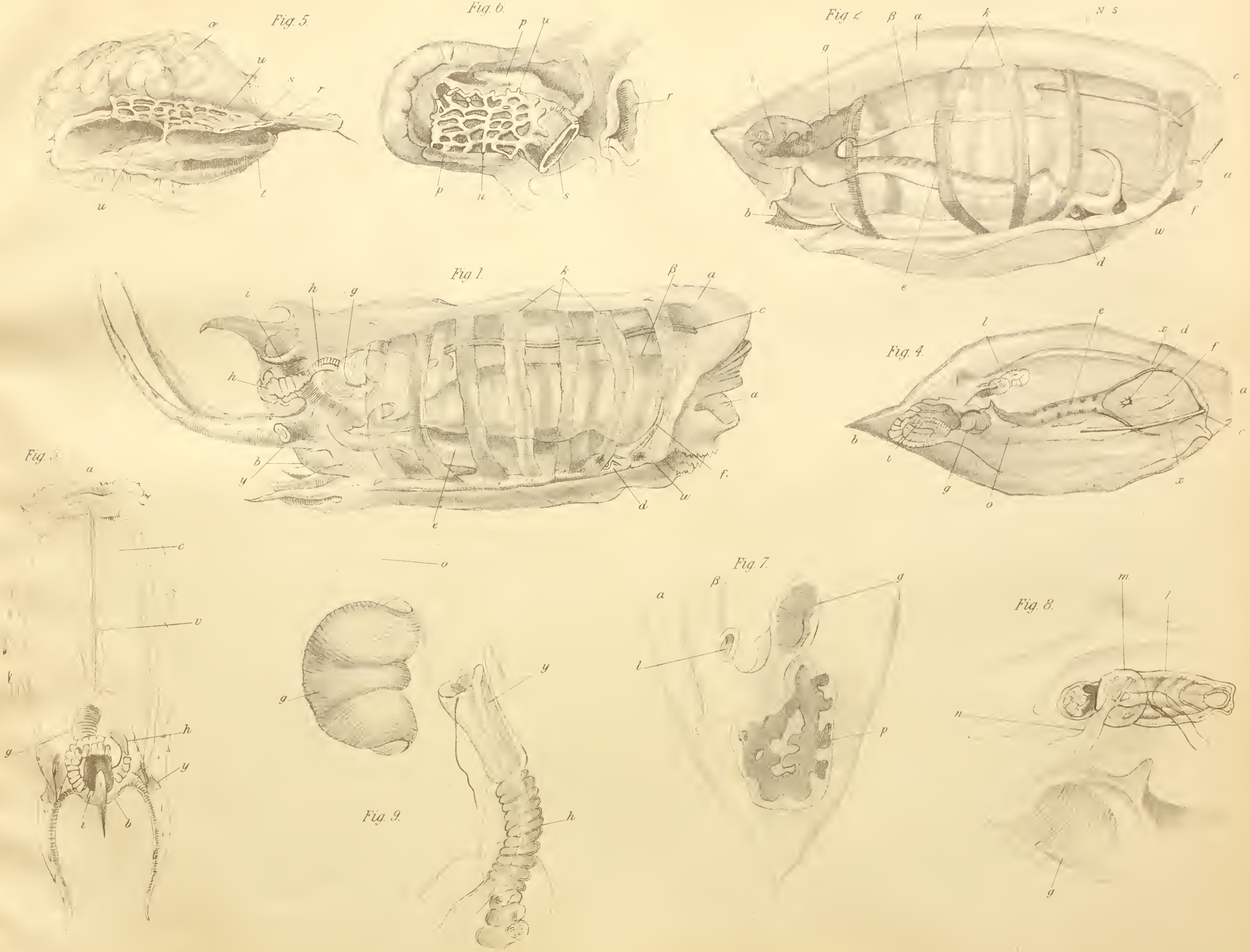


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Fig

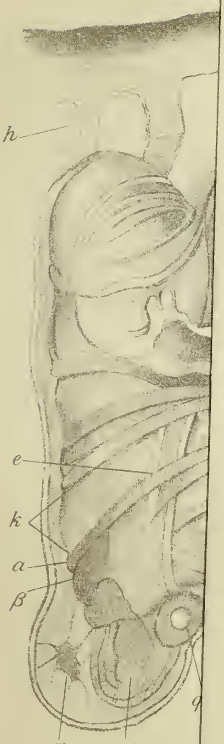


Fig. 4.

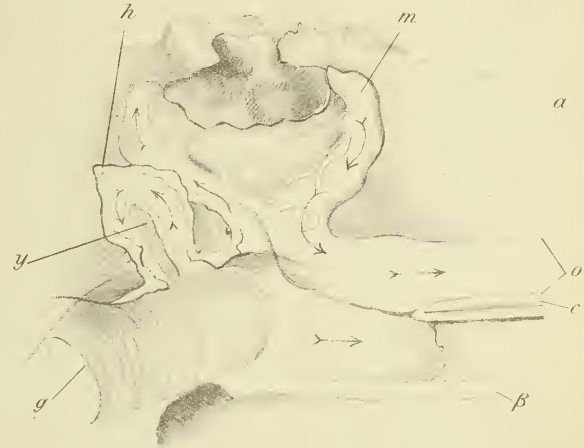
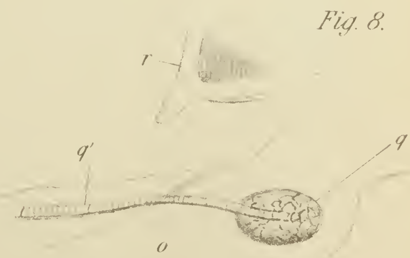


Fig. 3.a

Fig. 7.

Fig. 8.



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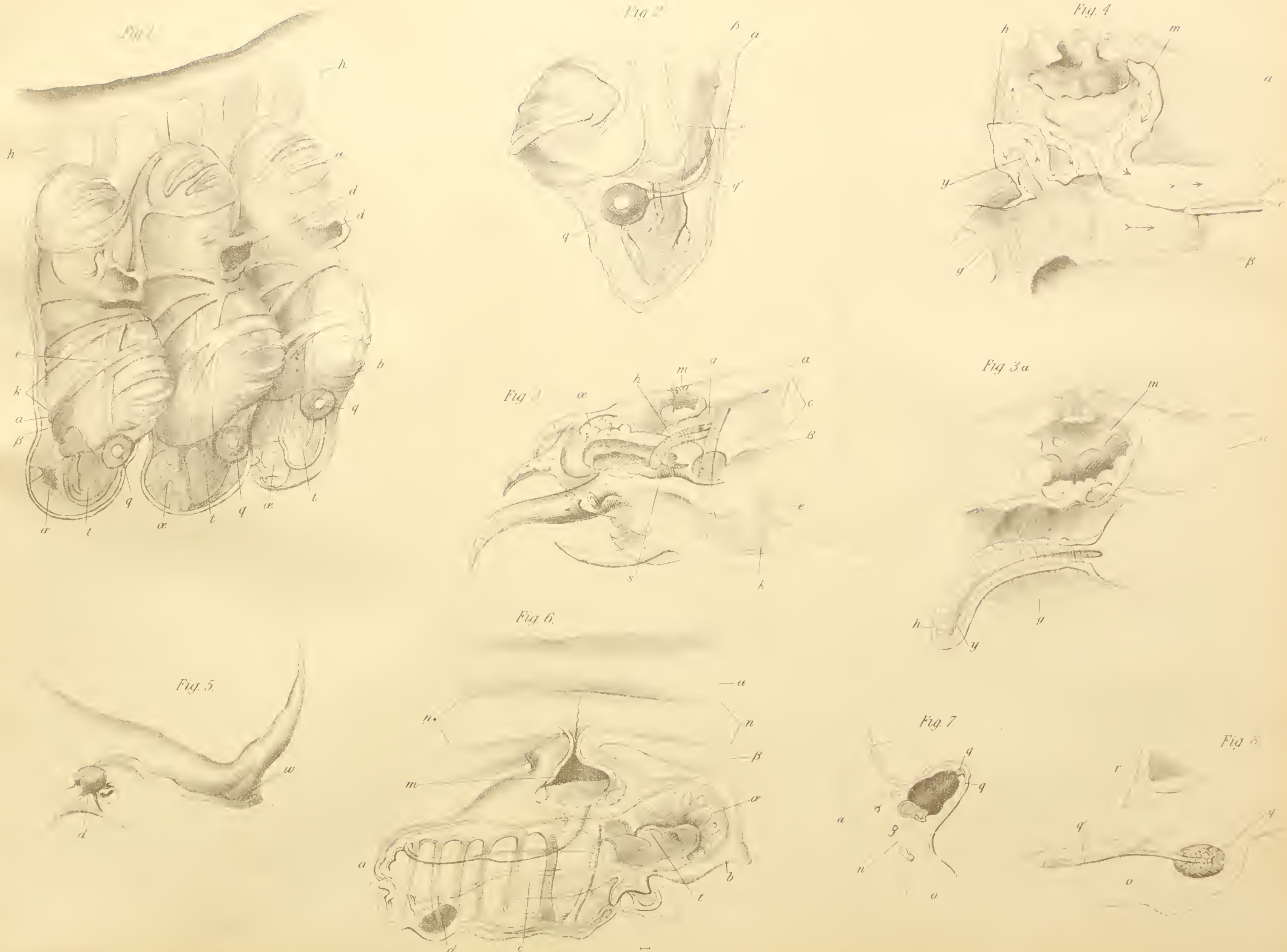


Ad. nat. del. T H H

Fig. 3.

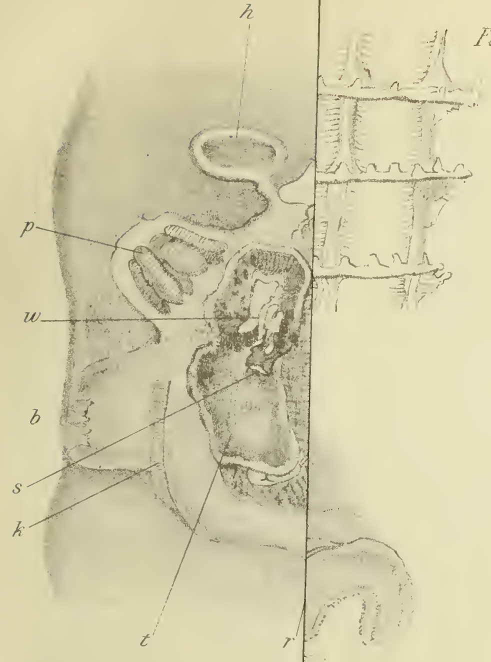


Fig. 10.

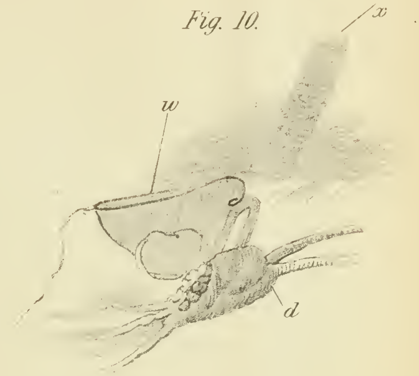


Fig. 5.

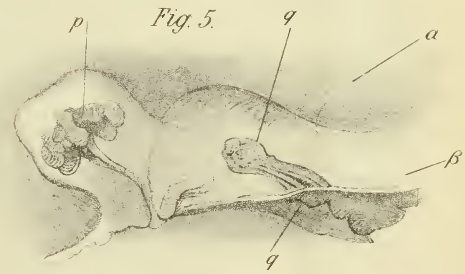
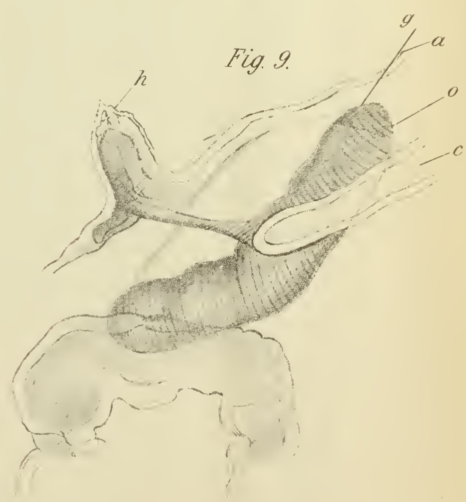


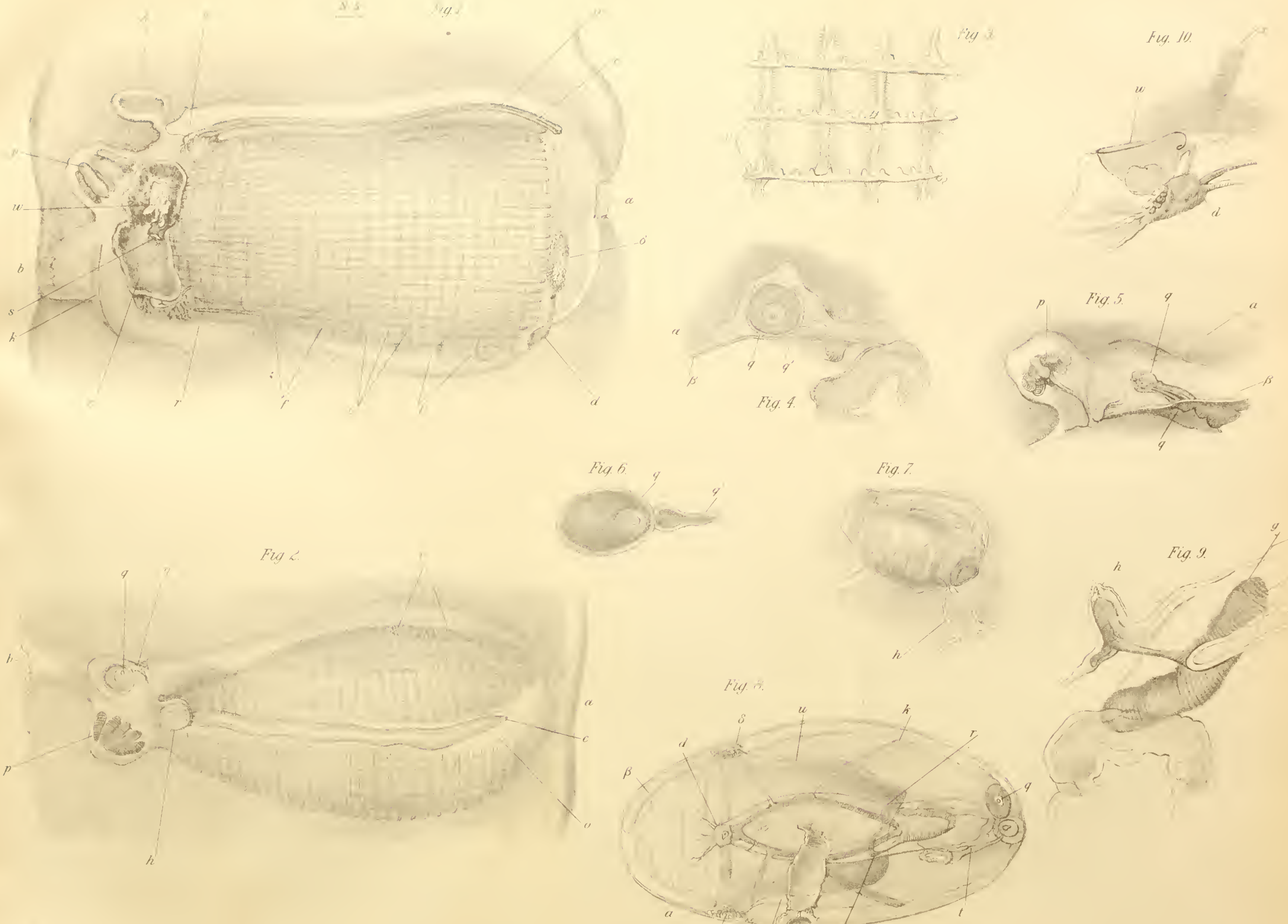
Fig. 7.

Fig. 9.



Ad. nat. del! T.H.H

Phil. Trans. MDCCCL. Plate



Ad nat. del! T H H

Fig. 4.

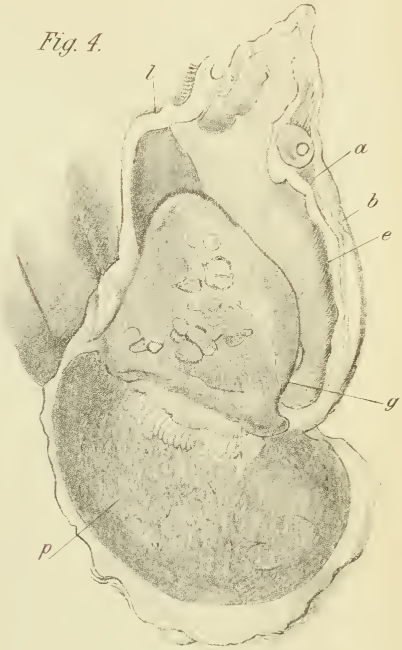


Fig. 2. a

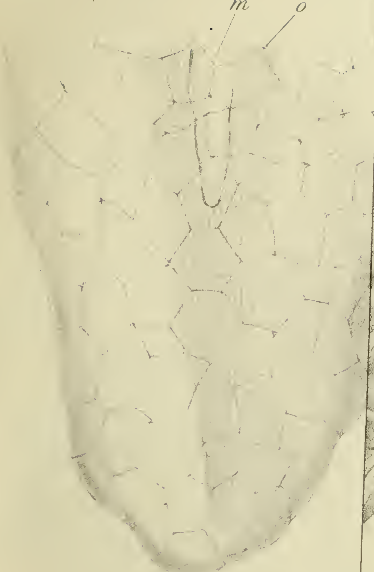
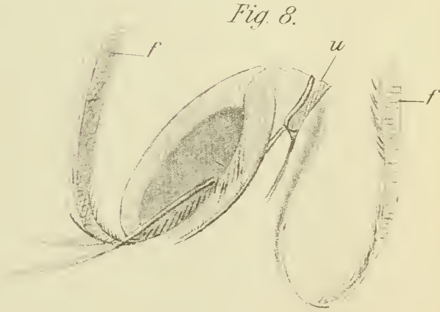


Fig. 3.

Fig. 8.



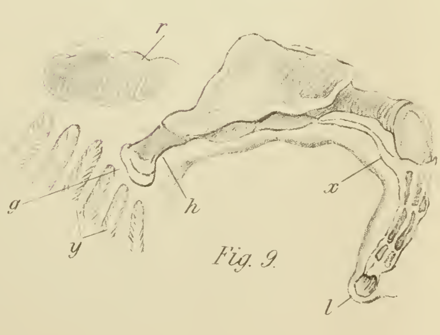
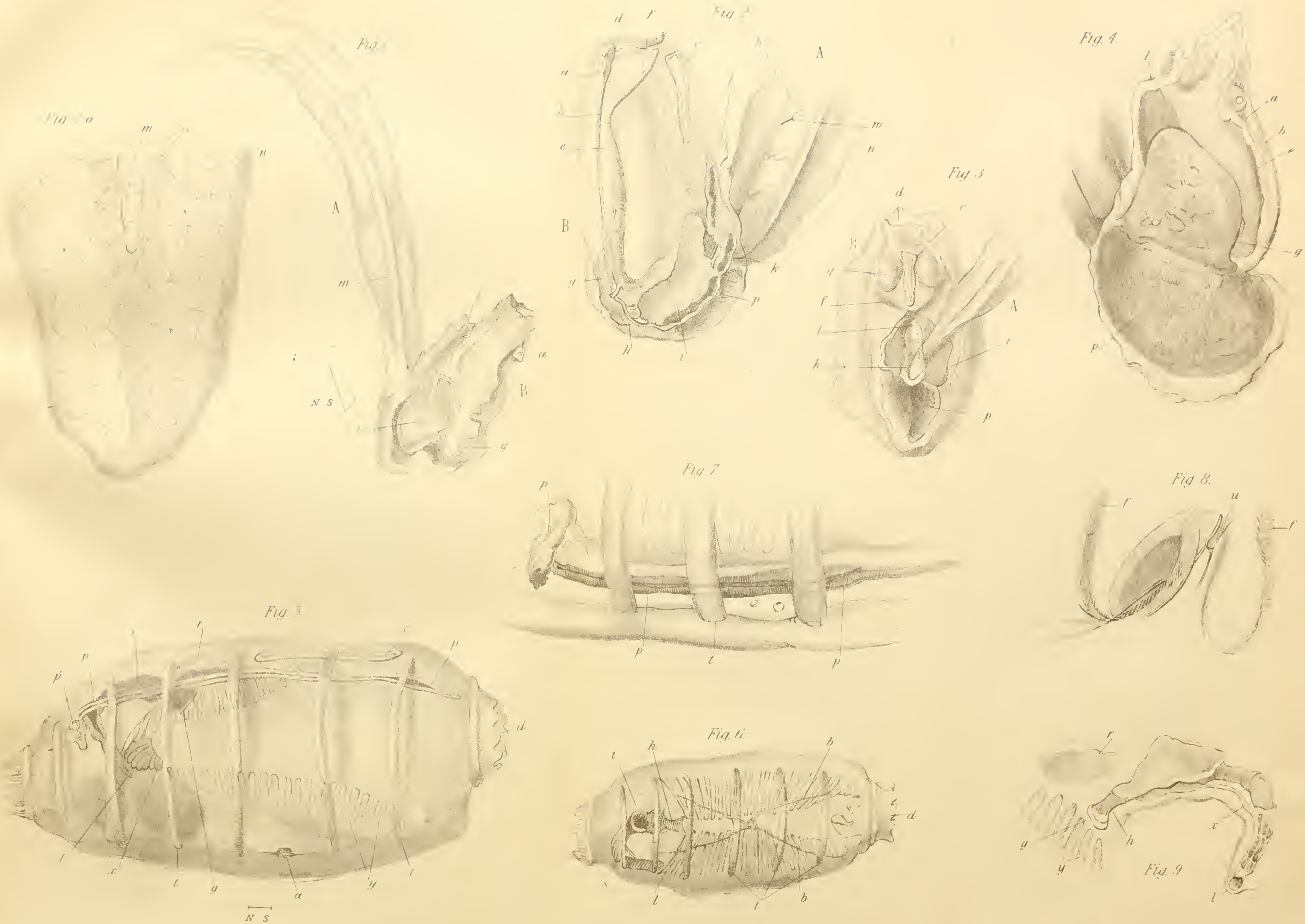


Fig. 9.

Ad. nat. del.t T.H.H.



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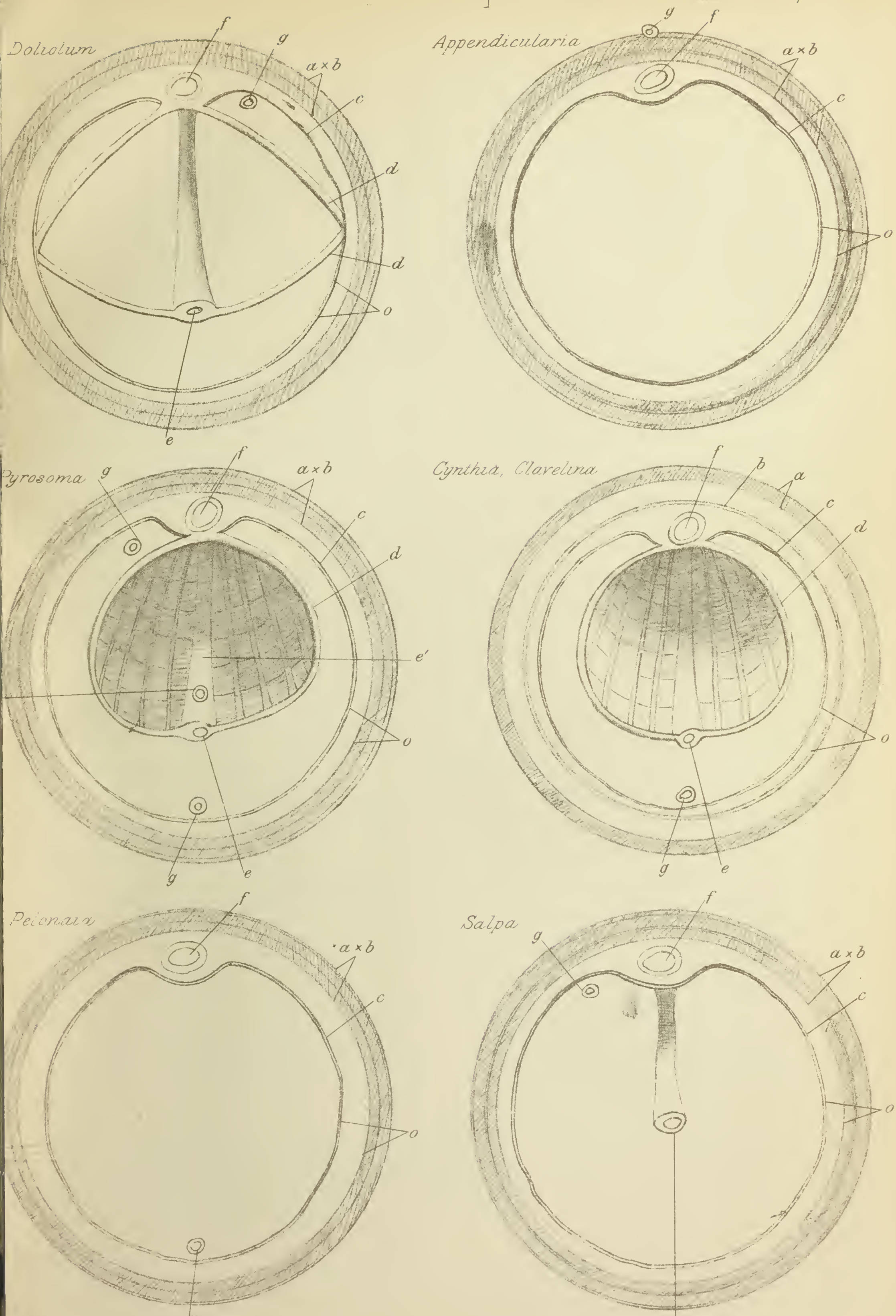
[PLATE IX.] *Phil. Trans. MDCCCLI. Plate XIX. p. 603*



a Test b outer tunic c inner tunic d branchial sac e epipharyngeal band.
ypopharyngeal band & Thoracic vessel f alimentary canal g Anus. h mouth o Sinus system

Sectional Diagrams of Tunicata.

The section supposed to be made perpendicular to the axis of the branchial cavity.

Fig. 8. A young zoöid separated and enlarged. Viewed from the ventral side.
Fig. 9. Youngest form of gemma observed.
Fig. 10. "Ciliated fossa," with the ganglion and otolithes.

a. Anterior extremity.
b. Posterior extremity.
c. Endostyle.
d. Ganglion and otolithes.
e. Gill band.
f. Languet.
g. Heart.
h. Gemmiferous tube (single gemma in *Pyrosoma*).
i. Nucleus.
k. Muscular bands.
l. Solitary fœtus, or young *Salpa* A.
m. Placenta.
n. Sinus running specially to the placenta.
o. Dorsal sinus.
p. Testis.
q. Ovary, or rather ovum.
q'. Pedicle.
r. Buccal orifice.
s. Anal orifice.
t. Lobe of the stomach.
u. Tubular system.
v. Branchial bars.
w. "Ciliated sac."
x. "Ciliated band."
æ. Eleoblast.
α. External tunic.
β. Internal tunic.
γ. Partition of gemmiferous tube.
δ. Cell masses in *Pyrosoma*.

Pl. XVIII. [Plate 8]

Fig. 1. *Appendicularia flagellum.* Much magnified.
Fig. 2. Still more magnified.
Fig. 2^a. Extremity of the caudal appendage.
Fig. 3. Body of *Appendicularia* from behind.
Fig. 4. Individual in which the testis is much enlarged.
Fig. 5. *Doliolum denticulatum*, from the right side.
Fig. 6. *Doliolum denticulatum*, from below.
Fig. 7. A portion of the right wall to show the testis *in situ*.
Fig. 8. The "ciliated sac" and the origin of the "ciliated bands" in *Doliolum*.
Fig. 9. The intestine and heart, with the commencement of the branchiæ.

The letters have throughout the same signification.

a. Ganglion with the auditory vesicle.
b. Nerve.
c. Endostyle.
d. Respiratory or anterior aperture.
e, f. Ciliated bands.
g. Mouth.
h. Œsophagus.
i. Stomach.
k. Intestine.
l. Anus.
m. Axis of the caudal appendage.
n. A long membrane of appendage.
o. Bundles of striated muscular fibrils.
p. Testis.
p'. Efferent duct of testis.
q. Supposed ovary.
r. Heart.
s. Liver.
t. Muscular bands.
u. Ciliated sac.
B. The body of *Appendicularia*.
A. The caudal appendage.
x. Hypopharyngeal band.
y. Branchial bars.
z. The system of tubules embracing the intestine.

Pl. XIX. [Plate 9]

The diagrams represent imaginary sections of the principal types of the Ascidian family. Without pretending to be strictly accurate, they are sufficiently so to give a just idea of the gradations in structure among the different genera, and of the essential unity of structure which runs through the group.

IX

ZOOLOGICAL NOTES AND OBSERVATIONS MADE ON BOARD H.M.S. RATTLESNAKE DURING THE YEARS 1846-50

Annals and Magazine of Natural History, vol. vii. ser. ii. 1851, *pp.* 304–6; 370–4; *vol. viii. pp.* 433–42

I. *On the Auditory Organs in the Crustacea.*

GREAT discrepancy prevails among the various authorities as to the true nature and position of the auditory organs in the Crustacea.

The older authors, Fabricius, Scarpa, Brandt, Treviranus, unanimously confer the title of auditory organs upon certain sacs filled with fluid which are seated in the basal joint of the second or larger pair of antennæ.

M. Milne-Edwards, in his elaborate researches upon the Crustacea,[1] adheres to this determination, and describes a very elaborate tympanic apparatus in the Brachyurous genus *Maia.*

By the majority of the earlier writers no notice is taken of the sac existing in many genera in the bases of the first or smaller pair of antennæ. Rosenthal[2] however describes this structure very carefully in *Astacus fluviatilis* and *Astacus marinus.* He considers it to be an olfactory organ, while he agrees with previous writers in considering the sac in the outer antennæ as the auditory organ.

Dr. Farre, in his admirable paper in the Philosophical Transactions for 1843, gives very good reasons for exactly reversing Rosenthal's denominations, and considering the sac in the first pair of antennæ to be the auditory organ, while the sac in the second pair is the olfactory organ. Dr. Farre doubts the existence of true auditory organs in the *Brachyura.*

Siebold in his Report upon the progress of the Anatomy of the

[1] Hist. Nat. des Crustacés. Suites à Buffon.

[2] Ueber die Geruchsorganen d. Insekten. Reil's Archiv, B. x. 1811.

Invertebrata for 1843-44,[1] mentions Dr. Farre's views, but seems to doubt their correctness ; and they have had no better reception from Prof. Van der Hoeven [2] and Erichson.[3]

The matter stands thus at present then. It is universally acknowledged that in the *Macroura* there exists in the basal joint of both the first and second pair of antennæ a sac containing a liquid, and that in the *Brachyura* such a sac exists at least in the second pair. According to the majority of authors the sac in the second pair is the auditory organ ; and according to Rosenthal the sac in the first pair is the olfactory organ.

On the other hand, if we take Dr. Farre's interpretation, the sac in the first pair of antennæ is the auditory organ, in the second the olfactory organ.

Although the structure of the organ contained in the first pair of antennæ in the *Macroura* departs somewhat from the ordinary construction of an acoustic apparatus in the Invertebrata, yet the argument from structure to function, as enunciated in the paper referred to, seems almost irresistible. Still, as it has obviously not produced general conviction, I hope that the following evidence may be considered as finally conclusive.

In a small transparent Crustacean (taken in the South Pacific) of the genus *Palæmon* (fig. 2 *a*), the basal joint of the first pair of antennæ is thick, and provided with a partially detached ciliated spine at the outer part of its base (fig. 3 *a*). Between this and the body of the joint there is a narrow fissure. The fissure leads into a pyriform cavity (fig. 3 *b*), contained within a membranous sac, which lies within the substance of the joint. The anterior extremity of the sac is enveloped in a mass of pigment-granules (*c*): on that side of the sac which is opposite to the fissure, a series of hairs with bulbous bases are attached along a curved line (*d*) ; these are in contact with, and appear to support, a large ovoidal strongly refracting otolithe (*e*).

The antennal nerve (*f*) passes internal to, and below the sac, and gives off branches which terminate at the curved line of the bases of the hairs.

The sac is about $\frac{1}{100}$th of an inch in length ; the otolithe about $\frac{1}{220}$th in diameter.

This structure is obviously very similar to the ordinary form of auditory apparatus in the Mollusca, &c. In *Lucifer typus* however we have an absolute identity.

In this singular crustacean (Pl. XIV. [Plate 10] fig. 1) the basal joint

[1] Müller's Archiv, 1845.

[2] Handbuch d. Zoologie, p. 597.

[3] Erichson's Archiv, 1844.

of the first or internal pair of antennæ is much longer than the others, and is slightly enlarged at its base. The enlargement contains a clear vesicle (*e*), slightly enlarged anteriorly, but not communicating by any fissure with the exterior. It is about $\frac{1}{600}$th of an inch in diameter. It contains a spherical strongly refracting otolithe about $\frac{1}{1250}$th of an inch in diameter, which does not present any vibrating or rotating motion. We have here then *Lucifer* presenting an organ precisely similar to the auditory sacs of the Mollusca, while *Palæmon* offers a very interesting transition between this and the ordinary crustacean form of acoustic organ as described by Farre, and there can I think be very little doubt that the determination of the latter (as regards the *Macroura* at least) was perfectly correct.

Since writing the above I find that the auditory organ in *Lucifer* has been recognized by M. Souleyet. All that he says about it is contained in the following lines:—"Bei einigen See-krustenthieren namentlich bei der Gattung *Lucifer* (Thompson) habe ich ganz neuerdings an der Wurzel der innern Fühler einen kleinen runden glänzenden Körper entdeckt der mir dasselbe Organ (auditory organ) zu seyn scheint."—*Froriep's Notizen*, 1843, p. 83.

EXPLANATION OF PLATE XIV. [Plate 10]

Fig. 1. The line indicates the natural size of the animal in this and the following figure: *a*, internal antennæ; *b*, external antennæ; *c*, basal lobe of external antennæ; *d*, eye; *e*, otolithic sac.

Fig. 2. Head of *Palæmon*. Letters as in fig. 1.

Fig. 3. Internal antennæ of *Palæmon* enlarged: *a*, spine; *b*, auditory sac; *c*, pigment-granules; *d*, curved line to which the hairs are attached; *e*, otolithe; *f*, antennal nerve.

II. *On the Anatomy of the genus* Tethya.

THE animal which forms the subject of the present communication was found attached to rocks and stones, close to low water mark, upon the shores (skirting one of the smaller bays of Sydney harbour) of the beautiful grounds of my friend Mr. W. S. MacLeay.[1]

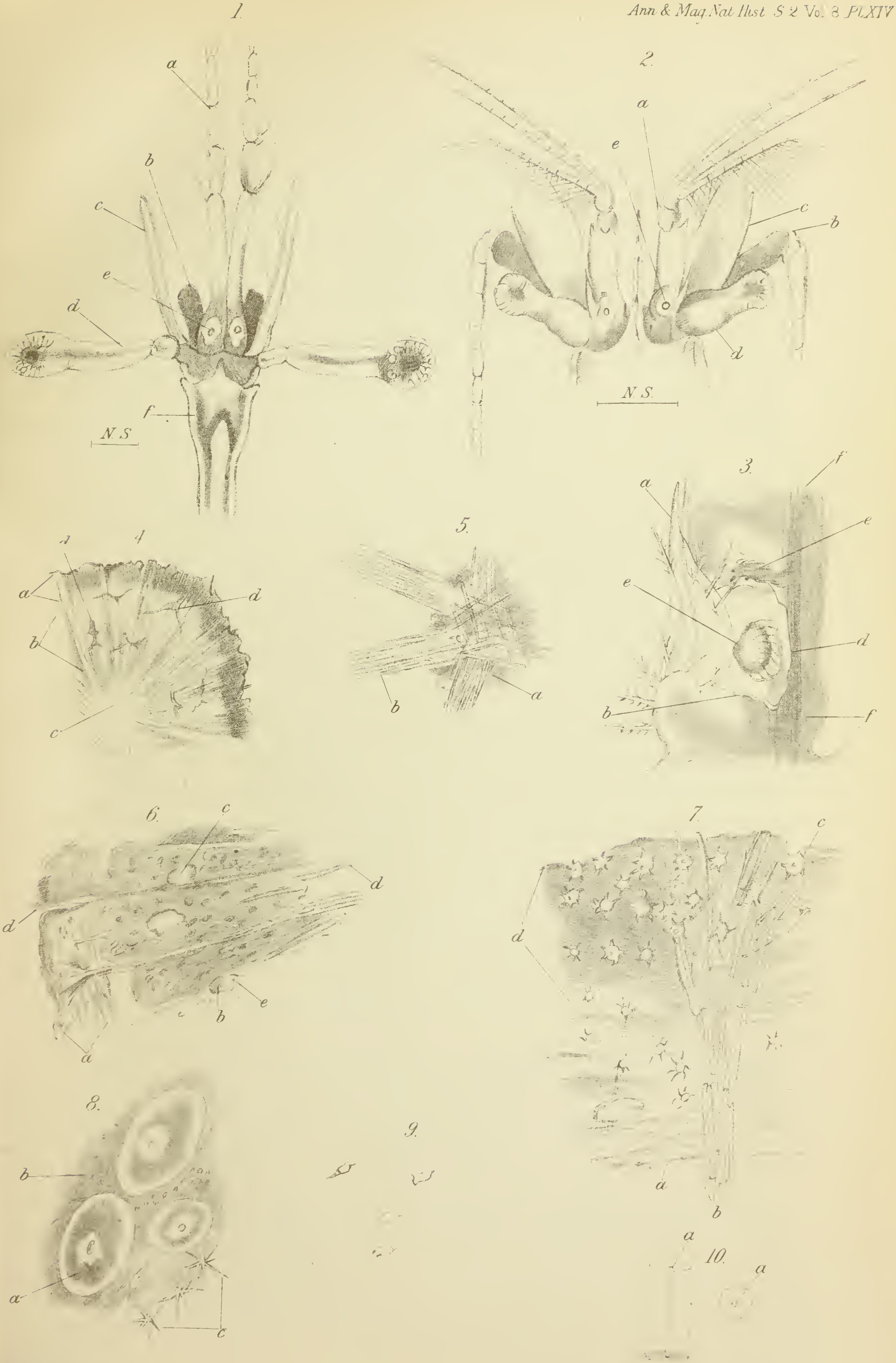
MM. Milne-Edwards and Audouin (Ann. d. Sc. Nat. 1828, tom. xv.) and Dr. Johnston (British Sponges and Lithophytes) are, so far as I am aware, the only authors who give any detailed account of the genus *Tethya*.

Of the two species described by the latter, *T. Lyncurium* approaches nearest to the present species; the only difference being that while

[1] It is not necessary for me to speak of Mr. MacLeay's singular acquirements and acumen; but I cannot refrain from taking this opportunity of expressing my deep sense of the benefit I have derived from his advice and assistance—always most readily offered.

[PLATE X.]

Ann & Mag. Nat. Hist. S. 2 Vo. 8 Pl. XIV



T. H. H. del.t

the former is yellowish white, the latter is deep red, and that the stellate bodies, scanty in the former, are very numerous in the latter.

However, pale specimens were frequent among the deep red ones—without any other apparent difference—and the presence of more or fewer stellate bodies is a mere question of degree.

MM. Edwards and Audouin describe currents traversing the "oscules" of the *Tethya* similar to those of a sponge. I did not observe any currents, but I do not doubt their existence.

Dr. Johnston says (*op. cit.* p. 82), "The propagation of *Tethya* is by means of sporules or gemmules generated within the sarcoid matter. The latter resemble the parent sponge in miniature, but they have no distinct rind or nucleus, being composed of simple spicula woven together by albuminous matter."

I did not observe such "sporules or gemmules" in any of the specimens I examined, but it can hardly be doubted that these bodies are merely further developments of the "ova" which I observed; and as I found spermatozoa, it will follow, that the *Tethyæ* are reproduced by a process of true sexual generation.

It would be most interesting to ascertain whether the "gemmules" of sponge take their origin in a similar way, and whether true spermatozoa are developed here also.

The specimens of *Tethyæ* observed presented several prominent tubercles upon their surface, perforated by irregular apertures, from which a liquid exuded when the animal was taken out of the water.

When there was only one or two of these tubercles, the external resemblance to some forms of *Cynthia* was very great.

On cutting across one of these bodies, it was seen to be solid, and composed of three distinct substances; viz. a central whitish spherical mass, a deep red cortical substance, and between these two, forming the largest part of the body, a yellowish red intermediate substance, sharply separated from both the central and cortical substances.

The two latter were united by radii of a silvery whitish colour, which ran through the intermediate yellow mass, and became lost in the cortical portion.

Small canals took their rise at the apertures already mentioned, and penetrating the cortical substance, ramified irregularly through the intermediate substance, reaching as far as, but not penetrating, the central substance. They appeared to be lined by a very delicate smooth membrane.

The general structure of the central, cortical, and intermediate portions agreed pretty closely with the description already given by Johnston.

1. *The central portion.*—This consists of a granular mass interpenetrated in every direction by short, cylindrical, transparent rods which form a sort of network. At the margins of the central portion, however, the rods become gathered into bundles, and they are longer and lie parallel to one another. In this form they enter the intermediate substance and form the radii before mentioned. When they reach the cortical substance, the majority of the rods diverge and become spread out; a few however remain as a bundle, and reach the edge, or even project a little beyond it.

Besides the bundles, a great number of long, solitary rods traverse the intermediate substance radially.

The rods are cylindrical, and about $\frac{1}{2500}$th of an inch in diameter. They are all perforated by a very narrow central canal, so as to appear like minute thermometer-tubes.

2. *The cortical substance* consists of two zones, an inner and an outer, which pass insensibly into one another at the line of contact.

The inner is composed of a mass of thick bundles of a fibrous tissue, so interwoven that a slice presents every possible section of them. The rods penetrate this zone, and a very few of the stellate bodies are found scattered through it.

The outer zone is dense, granular, and otherwise apparently structureless. Scattered through it are great numbers of crystalline spheres beset with short conical spikes.

3. *The intermediate substance.*—This consists of a granular substance in which ova and stellate crystalline bodies are imbedded.

The ova are of various sizes. The largest are oval and about $\frac{1}{330}$th of an inch in long diameter. They have a very distinct vitellary membrane, which contains an opake coarsely granular yelk. A clear circular space about $\frac{1}{1600}$th of an inch in diameter, marking the position of the germinal vesicle, is seen in the centre of each ovum, and within this a vesicular germinal spot $\frac{1}{5000}$th of an inch in diameter is sometimes visible, although with some difficulty, in consequence of the opacity of the yelk.

The stellate bodies are about $\frac{1}{1200}$th of an inch in diameter: they appear to be of a similar nature to those described in the cortical substance, but they are smaller; and while the radii are proportionally long, there is hardly any centre beyond that formed by their meeting.

The granular uniting substance is composed entirely of small circular cells about $\frac{1}{3300}$th of an inch in diameter, and of spermatozoa in every stage of development from those cells. The cell throws out a long filament which becomes the tail of the spermatozoon, and becoming longer and pointed forms, itself, the head.

The perfect spermatozoa have long, pointed, somewhat triangular heads about $\frac{1}{3000}$th of an inch in diameter, with truncated bases, from which a very long filiform tail proceeds.

It is remarkable that the ova are in no way separated from the spermatozoa, but lie imbedded in the spermatic mass like eggs packed in sand.

EXPLANATION OF PLATE XIV. [Plate 10]

Fig. 4. Section of *Tethya*; natural size: *a*, corticle substance; *b*, intermediate substance; *c*, central substance; *d*, canals.

Fig. 5. Portion of central substance (*a*) with two of the radii (*b*).

Fig. 6. Segment of the cortical and intermediate substances; *a*, cortical substance; *b*, intermediate substance; *c*, canals cut across; *d*, radii.

Fig. 7. A portion of the cortical substance: *a*, inner fibrous portion; *b*, radial bundle of rods; *c*, stellate bodies; *d*, marginal homogeneous portion.

Fig. 8. A portion of the intermediate substance: *a*, ova; *b*, granular substance consisting of spermatozoa and cells; *c*, stellate bodies.

Fig. 9. Spermatozoa in various stages of development.

Fig. 10. Longitudinal and transverse view of rods, showing the central canal, *a*.

Note—"Upon the Auditory Organ in Crustacea."

MM. Frey and Leuckart[1] (for access to whose work I am indebted to Prof. E. Forbes since writing on this subject) express a doubt as to the correctness of any of the determinations of the auditory organ in Crustacea hitherto given. They describe a very singular organ existing in the caudal appendages of *Mysis flexuosa*, consisting of an oval flattened sac or cavity $\frac{1}{3}$rd of a line in diameter, and containing an otolithe $\frac{1}{4}$–$\frac{1}{6}$th of a line in diameter. The otolithe is discoidal, flat on the one side, umbilicated on the other, and marked with concentric lines. About two-thirds of the circumference of the otolithe are occupied by the bases of a series of glassy, stiff hairs which are inserted into the otolithe and project from it.

The otolithe is apparently composed of chitine and carbonate of lime.

No nerve was traced to this sac, but the caudal ganglion is of large size.

No similar organ exists in *Palæmon*, *Crangon*, or *Squilla*, but the authors compare it to the organ noticed by Souleyet in *Lucifer*; and notwithstanding the extraordinary position of the organ, it must be allowed that its structure goes far to support this view. It must be remembered that in some of the lower Annelida the auditory organs are situated, not in the head, but one or two rings behind it, and in *Polyophthalmus* every ring has its pair of eyes.—See Quatrefages Ann. d. Sc. Nat. 1850.

[1] Beiträge zur Kenntniss Wirbelloser Thiere.

III. *Upon* Thalassicolla, *a new Zoophyte.*

In all the seas, whether extra-tropical or tropical, through which the Rattlesnake sailed, I found floating at the surface the peculiar gelatinous bodies which are the subject of the present communication. They were the most constant of all the various products of the towing-net, which was rarely used without obtaining some of them, and which sometimes, for days, would contain hardly anything else.

The extreme simplicity of structure of these creatures was more puzzling to me than any amount of complexity would have been. The difficulty of perceiving their relations with those forms of animal life with which I was familiar, gave me rather a distaste to the study of them, and, as I now perceive, has rendered my account of their organization far less complete than I could wish it.

However, these forms seem completely to have escaped the notice of voyagers, and therefore I hope to do some service by directing the attention of future investigators to them, and by endeavouring to show what seem to me to be their relations in the scale of being.

It may not be out of place at the same time to examine what are the *positive* characters of those lowest classes of animal life of which this is a member.

The *Thalassicolla*[1] is found in transparent, colourless, gelatinous masses of very various form ;—elliptically-elongated, hour-glass-shaped, contracted in several places, or spherical, varying in size from an inch in length downwards ; showing no evidence of contractility nor any power of locomotion, but floating passively on the surface of the water.

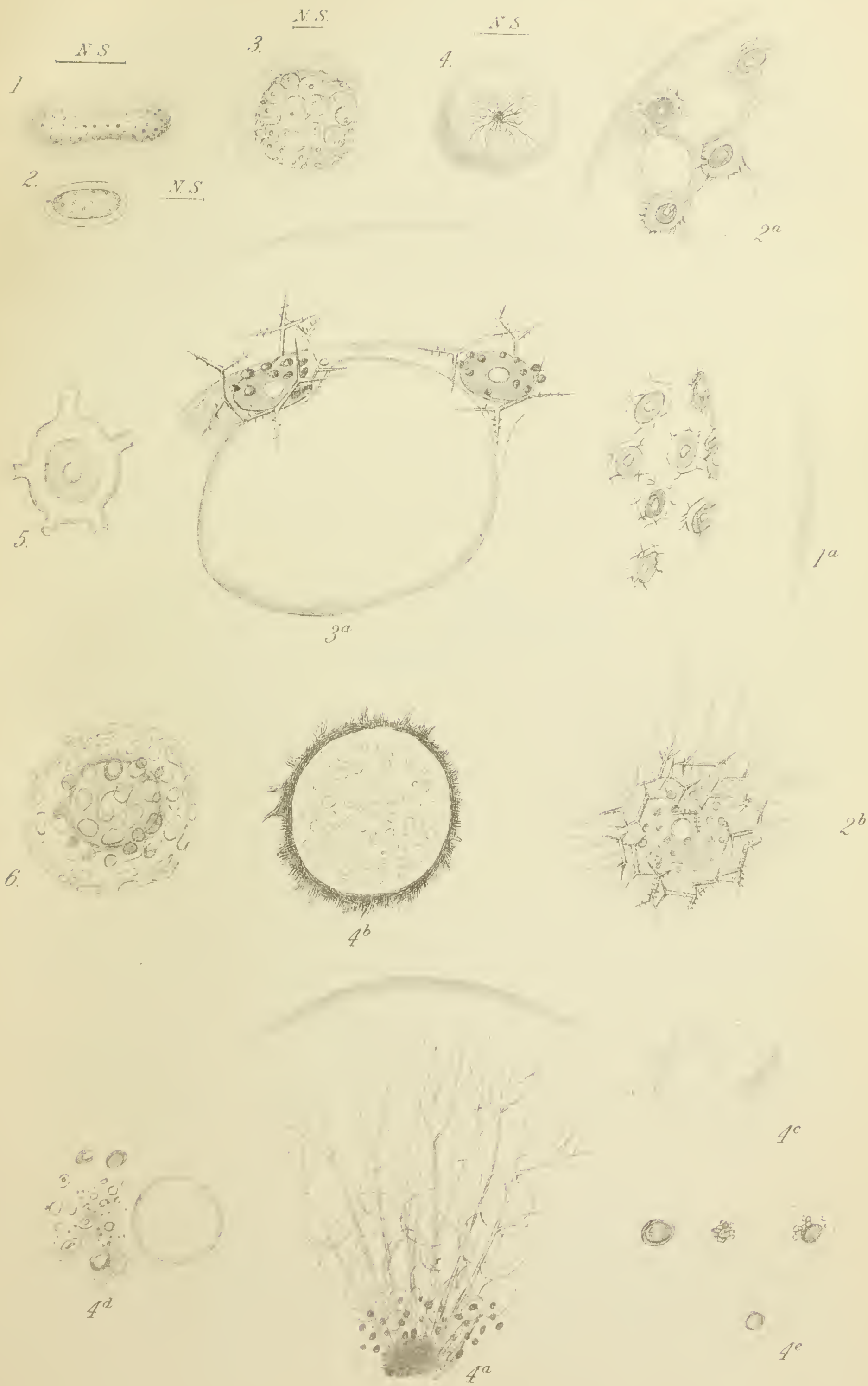
Now of such bodies as these there were two very distinct kinds : the one kind, consisting of all the oval or constricted, and many spherical masses, is distinguished to the naked eye by possessing many darker dots scattered about in its substance ; the smaller kind, always spherical, has no dots, but presents a very dark blackish centre, the periphery being more or less clear. I will adopt the provisional name of *Th. punctata* for the former kind, and that of *Th. nucleata* for the latter, as a mere matter of convenience, and without prejudging the question as to the existence of specific distinctions.

Th. punctata. (Pl. XVI. [Plate 11] figs. 1, 2, 3.)

The mass consists of a thick gelatinous crust containing a large cavity. The crust is structureless, but towards its inner surface minute

[1] θάλασσα, the sea ; κόλλα, jelly, glue.

[PLATE XI]



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spherical, spheroidal or oval bodies are imbedded, from which the appearance of dots arises. These are held together merely by the gelatinous substance, and have no other connexion with one another. Each "spheroid" is a cell, with a thin but dense membrane, $\frac{1}{200}$th to $\frac{1}{250}$th of an inch in diameter, and contains a clear, fatty-looking nucleus $\frac{1}{1400}$th to $\frac{1}{800}$th of an inch in diameter, surrounded by a mass of granules which sometimes appeared cellæform.

This fundamental structure—a mass of cells united by jelly—like an animal *Palmella*, was subject to many and important varieties.

Very commonly the central part of each mass, instead of containing a single large cavity, consisted of an aggregation of clear, large, closely-appressed spaces, like the "vacuolæ" of Dujardin (figs. 2, 3, 2 *a*, 3 *a*).

Very frequently also each cell was surrounded by a zone of peculiar crystals somewhat like the stellate spicula of sponge, consisting of a short cylinder, from each end of which three or four conical spicula radiated, each of these again bearing small lateral processes (figs. 3 *a*, 2 *b*).

In another kind, much more rarely met with, the spherical cell contained a few prismatic crystals about $\frac{1}{1000}$th of an inch in length; it was of a bluish colour, and enveloped in a layer of densely packed minute granules not more than $\frac{1}{15000}$th of an inch in diameter. Outside these there was a number of spherical bright yellow cells $\frac{1}{1600}$th of an inch in diameter, and inclosing the whole a clear, transparent brittle shell perforated by numerous rounded apertures, so as to have a fenestrated appearance (fig. 6). There were no spicula in this kind.

In a single specimen I found a similar shell, but its apertures were prolonged into short tubules (fig. 5).

Frequently the connecting substance in which the cells were imbedded appeared to be quite structureless, but in some specimens delicate, branching, minutely granular fibrils were to be seen radiating from each cell into the connecting substance (fig. 2 *b*).

I have mentioned certain minute bright yellow spherical cells contained within the shell of the fenestrated kind; such coloured cells are contained in all kinds either diffused through the connecting substance or more or less concentrated round each large cell (figs. 3 *a*, 2 *b*).

Th. nucleata. (Pl. XVI. [Plate 11] fig. 4.)

This form consists of a spherical mass of jelly as large as the middle-sized specimens of the last variety, with an irregular blackish central mass. Enveloping this and forming a zone about half the

diameter of the sphere there is a number of clear spaces—vacuolæ—varying in size from $\frac{1}{62}$nd to $\frac{1}{2500}$th of an inch, the smallest being innermost. Scattered among the vacuolæ of the innermost layer, there were many of the yellow cells, and a multitude of very small dark granules. Delicate, flattened, branching fibrils radiated from the innermost layer, passing between the vacuolæ, and in one specimen these fibrils were thickly beset with excessively minute dark granules, like elementary molecules, which were in active motion, as if circulating along the fibrils, but without any definite direction. In this case the whole body looked like a moss agate, so distinct were the radiating fibrils (4 *a*). Left to itself for less than an hour, however, this appearance as well as the circulation of granules vanished, and only a few scattered radiating fibrils were to be observed, the rest seeming to have broken off and become retracted.

By rolling under the compressor the outer mass could be completely separated from the central dark body, which then appeared as a spherical vesicle $\frac{1}{65}$th of an inch in diameter (fig. 4 *b*), showing obscurely a granular included substance.

The membrane of the vesicle was very strong, resisting, and elastic. When burst it wrinkled up into sharp folds (fig. 4 *c*), and gave exit to its contents (fig. 4 *d*). These were—

1. A very pale delicate vesicle (nucleus?) without any contents, and measuring (but when much compressed) about $\frac{1}{60}$th of an inch (fig. 4 *d*).

2. A heterogeneous mass consisting of (*a*) a finely granular base, (*b*) oil-globules of all sizes, (*c*) peculiar cells $\frac{1}{800}$th to $\frac{1}{1000}$th of an inch in diameter (4 *e*). Some of these had a solid greenish red nucleus about $\frac{1}{3500}$th of an inch in diameter. Others resembled the nuclei in colour and appearance, but were larger ($\frac{1}{2500}$th of an inch), and had no cell-membrane:—were these granule cells?

Altogether the *Thalassicolla nucleata* might readily be imagined to be a much enlarged condition of single cells of the *Th. punctata*; but I have no observations to show that it was so, nor can it be said from which of the varieties of *Th. punctata* the *Th. nucleata* arises.

The question may readily arise, Are these perfect forms? I can only say, as negative evidence, that I have never observed any trace of their further development, and that the spicula and 'shells,' and the capacity of fission, appear to afford positive grounds for believing that they are not mere transitional stages of any more highly-organized animal. If, further, it can be shown that their structure is closely allied to that of known organisms, this probability will, I think, almost amount to a certainty.

What animals are there then which consist either of simple cells or of cells aggregated together, which hold the same rank among animals that the Diatomaceæ and Desmidiæ, the Protococci and Palmellæ hold among plants?

Ten years ago the general reply of zoologists would have been—none. The researches of the celebrated Berlin microscopist, Prof. Ehrenberg (wonderful monuments of intense and unremitting labour, but at least as wonderful illustrations of what zoological and physiological reasoning should *not* be), led to the belief that the minutest monads had an organization as complicated as that of a worm or a snail. In spite, however, of the great weight of Prof. Ehrenberg's authority, dissentient whispers very early made themselves heard, from Dujardin, Focke, Meyen, Rymer Jones, and Siebold. To these Kölliker, Stein and others—in fact, I think I may say *all* the later observers—have added themselves, until it really becomes a matter of duty on the part of those interested in the progress of zoology to pronounce decidedly against the statements contained in the 'Infusionsthierchen,' so far as regards anatomical or physiological facts.[1]

It has been shown in the first place, that a great mass of the so-called Polygastria are plants—at any rate are more nearly allied to the vegetable than to the animal kingdom. Such is the case with the Diatomaceæ and Desmidiæ, the Volvocina, the Monadina, the Vibriones, and to these we must very probably add the Astasiæa.

So utter has been the want of critical discrimination in the construction of genera and species, that Cohn, in his admirable memoir upon *Protococcus pluvialis*, enumerates among the twenty-one forms (to which distinct names have been given by authors) assumed by the *Protococcus*, no less than *eight* of Prof. Ehrenberg's genera. The family "Polygastria," thus cut down to less than one-half its original dimensions, contains none but animals which are either simple nucleated cells, or such cells as have undergone a certain amount of change, not sufficient however to destroy their real homology with nucleated cells.

A nucleus has been found in *Euglena*, *Arcella*, *Amœba*, *Amphileptus*, *Trachelius*, *Bursaria*, *Paramœcium*, *Nassula*, *Chilodon*, *Oxytricha*, *Stylonichia*, *Stentor*, *Vorticella*, *Euplotes*, *Trichodina*, *Loxodes*, and other genera. It may be brought out by acetic acid just like any other nucleus in *Vorticella* and *Euglena*.

[1] That the above assertions will be considered by the majority of English readers to be unwarrantably severe, and considering the relative standing of the Professor and his critic, possibly impertinent, is no more than is to be expected.

I can only beg to disclaim all mere iconoclastic tendencies, and refer to a comparison of Prof. Ehrenberg's works with facts for my justification.

The animal is an unchanged cell in *Euglena*, in *Amœba* and in *Opalina*. In others, as the *Vorticellæ*, there is a more or less distinct permanent cavity in the interior of the cell which opens externally, an occurrence not without parallel among the secreting cells of insects. Certain genera, such as *Nassula*, have an armature of spines, but so have some of the Gregarinidæ which are unquestionably simple cells.

Contractile spaces,—cavities which appear and disappear in different parts of the Infusoria, and sometimes become filled with the ingesta,—are found no less commonly in the component cells of the tissues of many of the lower animals, and according to Cohn in the primordial cells of plants also.

The "Polygastria," then, may be justly considered to be simple cells, and to form a type perfectly comparable with *Thalassicolla*.

The researches of Henle, Stein, and Kölliker have made us acquainted with another form of cellular animals—the Gregarinidæ.

These are nucleated cells, without cilia, but with contractile walls, which lead an independent parasitic life in the intestines of many of the Invertebrata, principally insects.

The Gregarinidæ, like the Infusoria, are generally, if not invariably, single, solitary cells.

A third type is formed by the Foraminifera. The fate of these animals is somewhat singular. Considered to be Cephalopoda by D'Orbigny; Bryozoa by Ehrenberg; rudimentary Gasteropods by Agassiz; all careful observation tends to confirm the opinion of Dujardin, that the fabrication of their remarkable shells is essentially similar to *Amœba* and *Arcella*, both of which have been shown to be nucleated cells.

Lastly, we have the Sponges. That the tissue of the Sponges breaks up into masses, each of which is similar to an *Amœba*, has been pointed out by Dujardin, and confirmed by Carter and others. Dujardin, however, believing that a peculiar formless substance, "Sarcode," constitutes the tissues of the Sponges (as well as of the Infusoria and many other of the lower animals), fails to point out that they are mere aggregations of true cells.

This is not the place to discuss the important question, whether the great law developed by Schwann does or does not hold good among the whole of the lower animals. I believe that there is evidence to show that it does; that everywhere careful analysis will demonstrate the nucleated cell to be the ultimate histological element of the animal tissues; and that the "sarcode" of Dujardin, and the "formless contractile substance" of Ecker, are either cells or cell-contents, or the results of the metamorphosis of cells. Be this as it may, however, I

can say positively, as the result of recent careful examination, that *Spongilla*, *Halichondria*, and *Grantia* are entirely composed of nucleated cells.

The Foraminifera and Sponges then, no less than the Infusoria and Gregarinidæ, are "unicellular" animals—animals, that is, which either consist of a single cell, or of definite aggregations of such cells, none of which possesses powers or functions different from the rest.

Using the word "unicellular" in this extended sense (as it has been used by Nägeli and others with regard to the Algæ), it may be said that there are four families of unicellular animals; in two of these, the Infusoria and Gregarinidæ, the cells are isolated; in two, the Foraminifera and Sponges, they are aggregated together.

From these considerations it appears to me that the zoological meaning and importance of the *Thalassicolla punctata* first become obvious. It is the connecting link between the Sponges and the Foraminifera. Allied to the former by its texture and by the peculiar spicula scattered through the substance of some of its varieties, it is equally connected with the latter by the perforated shell of other kinds. If it be supposed that a *Thalassicolla* becomes flattened out, and that a deposit takes place not only round the cells, but between the partitions of the central "vacuolæ," it becomes essentially an *Orbitoides*.[1]

To come to a similar understanding of the nature of the *Thalassicolla nucleata*, it is necessary to recur again to certain general characteristics of the reproductive processes in the unicellular animals.

If we except *Tethya*, a sponge,[2] the ordinary reproductive elements have as yet been found in no unicellular animal.

Fission occurs in all except perhaps the Gregarinidæ. Gemmation appears to take place in the Foraminifera and Infusoria. In the Sponges the so-called ova or gemmules seem to be only a temporary locomotive condition of the cells, such as occurs in the *Vorticellæ* among the Infusoria, and the *Protococci* among plants.

But in all (except the Foraminifera) a process of multiplication by

[1] Dr. Carpenter, to whom I communicated these observations, writes to me: "As far as I can understand them, the bodies described (if perfect non-embryonic forms) seem to constitute that kind of connecting link between Sponges and Foraminifera, which the relative position I have assigned to them would lead me to expect. It is interesting to remark that the cullender-like skeleton of certain Foraminifera is extremely like in its appearance to a fragment of the shell of an Echinus, or to the plates contained in the integument of a Holothuria, and we know that these begin with a network of spicules. Consequently there is not by any means so great a distinction between the spicular skeleton of a sponge and the cullender-like skeleton of an Orbitolina as might at first sight appear."

[2] See Annals of Nat. History, S. 2, vol. vii. p. 370.

endogenous development occurs, and would seem in some cases to represent sexual propagation. Now the mode of this endogenous multiplication presents remarkable features of similarity in the Infusoria, the Gregarinidæ, and the Sponges.

There is a certain period in the existence of *Vaginicola crystallina*, when, gorged with food stored up in the shape of fat granules, &c., within the cavity of its cell-body, it becomes sluggish and eventually still. The body contracts and becomes rounded, and the transparent case closes in and seals up its inhabitant. Eventually long processes are developed from the body, and it takes on the form of the genus *Acineta* of Ehrenberg. After a while a new life stirs within this chrysalis-like form, and the contained mass gives rise successively (by a sort of fission) to young ciliated bodies, which leave the *Acineta* and become *Vaginicolæ*.

In a similar manner *Vorticella microstoma* becomes *Podophrya fixa*; but sometimes the changed *Vorticella* has no stalk, and then is the *Actinophrys* of some authors (not *A. Sol*). It is not known in what way the embryos are brought forth here, but it is a very significant fact that both the stalked and unstalked forms have been observed to conjugate.

Epistylis presents similar phænomena.

The *Actinophrys Sol*, to which more particular reference will be made by and by, has been observed to conjugate, but it is not absolutely known to arise by the metamorphosis of any *Vorticella*, though there is every probability in favour of the supposition that it does.

The Gregarinidæ pass through similar changes. Two forms of these creatures are known; the one consisting of protean nucleated cells, the other of motionless spherical sacs, containing a vast number of minute bodies resembling *Naviculæ* in shape, and thence called "Navicella-sacs." Now, according to Stein, although the fact has been doubted by others, the "Navicella-sacs" result from the conjugation of two *Gregarinæ*, which have become motionless and filled with an accumulation of granules.

Certain it is that the Navicellæ are developed within the granular mass like embryo-cells within the yelk, and that when freed by the bursting of the Navicella-sac they become *Gregarinæ*.

Lastly, in the freshwater sponge (*Spongilla*), which consists of an aggregation of nucleated protean cells like a mass of *Gregarinæ*, a certain number of the cells at various points scattered through the substance of the *Spongilla* become motionless and distended with granules, and receiving first a membranous and then a siliceous investment, constitute the "seed-like bodies."

From Mr. Carter's account it would appear that when the "seed-like body" germinates its cells burst, and their granular contents become mixed. Subsequently protean cells, like the ordinary sponge-cells, make their appearance *pari passu* with the disappearance of the granules.

Supposing this account to be correct, the conjugation in *Spongilla* would be perfectly analogous to that of the Desmidiæ and Diatomaceæ, while in the Infusoria and Gregarinidæ it would resemble that of *Zygnema.*

Generalizing the above details (full authority for which may be found in the appended list of works), we may say that with the exception of the Foraminifera, about whose reproductive processes nothing is as yet known, the Protozoa all reproduce their kind by a process of endogenous development which is accompanied by greater or less changes in the structure and powers of the reproducing cell. We may add that in many cases these changed cells have been observed to conjugate, previous to the occurrence of the endogenous development.

Bearing all these facts in mind, let us return to *Thalassicolla nucleata.* If the *Th. punctata* answer to a mass of sponge-cells, or an aggregation of *Gregarinæ*, is it not possible that the *Th. nucleata* may answer to the altered reproductive cell? I have shown that the *Th. nucleata* may very possibly be nothing more than a separated and enlarged cell of *Th. punctata*, and this possibility upon structural grounds becomes, I think, converted into probability, if *Th. nucleata* be compared with *Actinophrys Sol*, which there is every reason to believe is the reproductive stage of one of the Vorticellinæ.

Actinophrys Sol is a spherical gelatinous mass consisting of an internal dark granular portion and a clearer external zone from which many radiating threads are given off. Vacuolæ are scattered through the substance, larger in the external zone, smaller and more irregular in the interior.

If the animal is much compressed, nuclei and nucleated cells are forced out from its interior.

Finally, two specimens of *Actinophrys* have been observed to fuse together and become one.

It is unnecessary to point out the perfect analogy between *Actinophrys* and *Thalassicolla nucleata*, with one exception, that the large internal cell was not observed in *Actinophrys*—a circumstance which might readily occur if it were delicate, even though it existed.

The argument derived from this analogy becomes still more strengthened if we turn to the excellent account of *Noctiluca*—a marine phosphorescent body which has long been a zoological puzzle

—by M. de Quatrefages. For the details I must refer to that observer's paper in the 'Annales des Sciences,' but I may state that its structure is essentially similar to that of *Thalassicolla nucleata*, supposing that the latter had given exit to its central cell by a depression at one point of its surface. *Noctiluca*, however, appears to feed after the manner of *Actinophrys*, and perhaps conjugates also, as M. de Quatrefages "has met with double individuals two or three times." This he considers an evidence of spontaneous fission; but further observation might have reversed this judgement, as it did that of Kölliker with regard to *Actinophrys*.

From the invariable adhesion of grains of sand to one part of the surface of *Noctiluca*, it would seem to be set free from some unknown fixed form which is probably analogous in its structure to *Thalassicolla punctata*.

To sum up the different lines of argument it may be said—

1. That the *Thalassicolla punctata* is not an exceptional form of animal life, but belongs to the same great division as the Sponges, Foraminifera, Infusoria, and Gregarinidæ,—the Protozoa or unicellular animals.

2. That the Protozoa have definite characters as a class, which are—

a. That they are either simple nucleated cells or aggregations of such cells, which are not subordinated to a common life.

b. That they have a mode of reproduction consisting in an endogenous development of cells, preceded by a process analogous to the conjugation of the lower plants.

3. That the *Thalassicolla nucleata* closely resembles *Actinophrys Sol*, which is known to conjugate, and which there is great reason to believe is the reproductive stage of one of the Vorticellinæ.

4. That as *Th. punctata* is one of the Protozoa, it most probably has a reproductive stage.

5. That *Th. nucleata* might readily be derived from such an alteration in one of the cells of *Th. punctata* as occurs in the sponge-cells when they go to form the seed-like body, or in the Gregarina-cells when they become "Navicella-sacs."

6. That *Thalassicolla nucleata* is essentially similar in structure to *Noctiluca*.

Finally, I may be permitted to say, that no one can be more fully conscious than myself of the slender and hypothetical grounds on which some of these conclusions rest. My chief purpose has been

merely to show the tendency of the evidence now extant as clearly and broadly as possible ;—rather to draw out a brief than to pronounce a judgment.

The following are the authorities referred to in the text :—

Von Siebold. Vergleichende Anatomie d. Wirbellosen Thiere, p. 7–25.

——— Ueber einzellige Pflanzen u. Thiere. *Siebold und Kölliker's Zeitschrift*, 1849.

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Quatrefages. Observations sur les Noctiluques. *Annales des Sciences*, 1851.

Hogg. Upon Spongilla. *Trans. Linn. Soc.* vol. xviii.

Carter. On Spongilla. *Annals of Nat. Hist.* 1849.

X

OBSERVATIONS ON THE GENUS SAGITTA.

British Association Report, 1851, *pt. ii. pp.* 77–78 (*Sectional Transactions*).

MR. HUXLEY made some observations upon the structure of the anomalous genus *Sagitta*, which has already been more than once a subject of discussion at the Meetings of the British Association. Mr. Huxley's statements essentially confirmed those of M. Krohn; the existence of a ciliated canal or oviduct in the outer part of the ovary being the only new fact of any importance brought forward. The very wide geographical distribution of *Sagitta* was alluded to, the animal having been found in all the seas through which H.M.S. Rattlesnake passed in her circumnavigatory voyage.

In discussing the zoological relations of *Sagitta*, Mr. Huxley's remarks were to the following effect:—*Sagitta* has been placed by some naturalists among the Mollusca, a view based upon certain apparent resemblances with the Heteropoda. These however are superficial; the buccal armature of *Sagitta*, for instance, is a widely different structure from the tongue of Firola, to which, when exserted, it may have a distant resemblance; the distinct striation of the muscular fibre, and the nature of the nervous system, equally separate *Sagitta* from the Mollusca.

There appears to be much more reason for placing this creature, as Krohn, Grube, and others have already done, upon the annulose side of the animal kingdom, but it is very difficult to say in what division of that sub-kingdom it may most naturally be arranged. At first sight it seems to present equally strong affinities with four principal groups, viz.—1. the Nematoid worms; 2. the Annelida; 3. the Lernæan Crustacea; and 4. the Arachnida.

1. With the Nematoid worms it is allied by its general shape and habit, its want of distinct annulation, and remotely, by the armature

of the mouth. But on the other hand, it differs widely from them in the nervous system, the sexual system, and the nature of the muscular tissue.

2. *Sagitta* has no small resemblance to certain Naiadæ, in which when young the anterior hook-like feet are directed forwards parallel to the mouth. It differs from them in the nature of its nervous system, which exhibits a concentration quite foreign to the annelid type, in the nature of the muscular tissue, and in the total absence of any water vascular system.

3. and 4. The real affinities of *Sagitta* are probably with one or other of these great divisions. The structure of the nervous and muscular system speaks strongly for this view, and the nature of the sexual system is not opposed to it, inasmuch as we have hermaphrodism among both the lowest Crustacea (Cirrhipedia) and the lowest Arachnida (Tardigrada).

The study of development can alone decide to which of these divisions *Sagitta* belongs; but until such study shall have demonstrated the contrary, Mr. Huxley stated his belief that *Sagitta* bears the same relation to the Tardigrada and Acaridæ, that Linguatula (as has been shown by Van Beneden) bears to the genus *Anchorella*, and that the young *Sagitta* will therefore very possibly be found to resemble one of the Tardigrada, the rudimentary feet with their hooks being subsequently thrown up to the region of the head, as they are in Linguatula.

XI

AN ACCOUNT OF RESEARCHES INTO THE ANATOMY OF THE HYDROSTATIC ACALEPHÆ.

British Association Report 1851, *pt.* 2, *pp.* 78–80

THE observations upon which this communication is based were made during the circumnavigatory voyage of H.M.S. Rattlesnake, but for the most part in the seas which border the coasts of North-eastern Australia, New Guinea, and the Louisiade archipelago.

With the exception of the mere external form, but very little has been known hitherto with regard to either the Diphydæ or the Physophoridæ, the two families of which the 'Hydrostatic Acalephæ' of Cuvier consist, although they are some of the most abundant of pelagic creatures. Indeed, hardly any one can have made a voyage to the East Indies or Australia without being struck with the immense shoals of the *Physalia* and *Velella*, through which the ship sometimes sails for days together.

The chief mass of one of the Diphydæ is formed by two transparent crystalline pieces, which look, when taken out of the water, like morsels of cut glass. One or both of these pieces contains a wide cavity, lined by a muscular membrane, by the contraction of which the animal is propelled through the water. The attachment of the posterior piece to the anterior is very slight, and when detached it will swim about independently for hours together. It was this circumstance which led Cuvier to consider the two pieces as two distinct animals.

In the Monogastric Diphydæ a single polype is developed in a special cavity of the anterior piece. In the Polygastric Diphydæ, a long chain of such polypes, each enveloped in a little transparent "bract," occupies a similar position. These polypes have no oral entacles, but a long thread-like tentacle, bearing lateral branches,

which are terminated by small sacs, is developed from the base of every polype. The small "prehensile" sac has a very peculiar form, but is, morphologically, only a dilatation of its pedicle, one wall of which is much thickened, and contains a great number of such urticating organs or "thread-cells" as are found among the Medusæ. The reproductive organs are medusiform bodies which are developed by gemmation from the pedicle of the polype.

The central sac of the medusiform body, instead of becoming a stomach, developes the spermatozoa or ova within its walls. These are generally shed forth while the organ is still attached, but in one genus they swim about independently, and might readily be mistaken for Medusæ.

In the Polygastric Diphydæ new polypes are continually being produced by gemmation at the attached extremity of the polype chain, and in both polygastric and monogastric forms, the same gemmation is continually going on among the prehensile and reproductive organs. The gemmæ, whether they are eventually to become polypes, prehensile organs, or reproductive organs, are invariably at first simple, double-walled processes, containing a cavity continuous with that of the common stem of the animal, which is itself a double-walled tube. The Diphydæ, whether polygastric or monogastric, are invariably diœcious.

The genus *Rosacea*, among the Polygastric Diphydæ, is remarkable in possessing only the anterior piece, which is gelatinous and hemispherical, like the umbrel of a *Medusa*. If a peculiar dilatation—the float—were formed at the extremity of the polype-chain of a Diphyes, we should have one of the Physophoridæ.

The genera *Rhizophysa*, *Physalia*, *Athorybia*, *Physophora*, *Stephanomia*, *Agalma*, *Porpita*, and *Velella*, were described and their structure illustrated by diagrams, without which the details would be unintelligible. Suffice it to say, that their forms, however varied, are shown to be simple modifications of a common type, in the main identical with that of the Diphydæ. Thus, such a polype-chain as that of *Rosacea*, if it developed a float, would be a *Rhizophysa*. The *Physalia* is a *Rhizophysa* with its float disproportionately enlarged; the *Physophora*, a *Rhizophysa* which has developed lateral natatorial organs like those of a Diphyes. Again, the *Velella* may be considered as a *Physalia* flattened out and having its air-sac divided and subdivided by partitions, until it becomes a firm, resisting, internal shell.

The same continual multiplication of parts by gemmation goes on among the Physophoridæ as among the Diphydæ; and the structure and mode of development of the young organs is essentially the

same. Great variety is presented by the reproductive organs, from the form of mere sacs to that of free-swimming bodies, precisely resembling Medusæ, and developing the generative elements only subsequently to their liberation. In *Physalia*, the female organs are free-swimming medusiform bodies, while the male organs are simple pyriform sacs, which remain attached and develope their spermatozoa *in situ*. In the language of the "alternation theory," the *Physalia* itself and the medusiform body would be two generations, and we should be presented with the unexampled peculiarity of a male giving birth to a female.

As a general conclusion, it may be stated that the Diphydæ and Physophoridæ are essentially composed of two membranes, an outer and an inner, which the author calls "foundation-membranes," since every organ is formed by the modelling into shape of one or other, or both of these, commencing as a simple process or diverticulum, and assuming its perfect form by a gradual differentiation. The stomach has no walls distinct from those of the general parietes. The reproductive organs are always developed externally, and the thread-cell is found in all in the greatest abundance. The author lays particular stress on the bearing of the latter fact upon classification, and shows that the same organ is met with in equal abundance only in the Hydroid and Sertularian Polypes, the Medusidæ, Beroidæ, and Anthozoic Polypes. A similar organ has indeed been also found in an Echinoderm, in certain Trematoda, and perhaps, although the author is inclined to think that its presence in this case is accidental, in Eolis; but in none does it assume such a prominent place as in the families mentioned.

The author endeavours to show that this fact, combined with the radiate polype form, and the composition of the body of two distinct membranes, forms a very good *positive* character for a group embracing the Hydroid and Anthozoic Polpyes, and the Acalephæ; a group equal in importance to any one of the primary subdivisions of the animal kingdom. The name of *Nematophora*, "thread-bearers," is proposed for this group, in allusion to the characteristic diffusion of the "*thread*-cell." But this group must be subdivided into two equivalent sub-classes. In the Hydroid Polypes, the Diphydæ, Physophoridæ, and Medusidæ, the stomach is *not distinct* from the common parietes, and the reproductive organs are *external*. In the Anthozoic Polypes and Beroidæ, the stomach *is distinct* from the common parietes, and the reproductive organs are *internal*. Some years ago Mr. W. S. MacLeay, when consulted by the author, suggested the name of *Œcioa* (those which have their eggs under cover,

"housed"), for the latter division, and that of *Anœcioa* for the former. Now a mutual representation runs through these two groups. For instance, the Actinidæ represent the Hydra and its allies; the Zoanthidæ represent the Corynidæ; the Physophoridæ seem to represent the Pennatulidæ; and the Medusidæ, the Beroidæ. Furthermore, each group returns into itself; the free floating Actiniæ nearly approximate Beröe, and *Lucernaria* is but a fixed *Medusa*.

Should these considerations eventually prove to be well-founded, the author considers that it will be necessary to break up the class Radiata of Cuvier into four groups, severally capable of being defined by positive characters. Supposing the Nematophora to form a sort of central group, we have on the one hand the Ascidians and the Bryozoa, leading to the Mollusca; on the other the Echinoderms and Entozoa (in the widest sense), leading to the Annulosa; whilst the Polygastria, Sponges, and Gregarinidæ (if indeed they are not rather to be considered only as the lowest forms of the other three groups) conduct us towards the lowest plants. These relations may be thus represented:—

MOLLUSCA. ANNULOSA.

Ascidians. Bryozoa. Echinodermata. Entozoa.

R A D I A T A.

NEMATOPHORA.

Anœcioa. Œcioa.

PROTOZOA.

Polygastria. Spongiadæ. Gregarinidæ.

PROTOPHYTA

XII

DESCRIPTION OF A NEW FORM OF SPONGE-LIKE ANIMAL.

British Association Report 1851, *pt.* 2, *p.* 80

THE author described a gelatinous substance found in almost all seas, in masses varying in size from that of a pea to that of a walnut. This mass is an animal of extreme simplicity, analogous to the Palmellæ in the vegetable kingdom, and consisting of a number of simple cells united by a gelatinous connecting matter, containing siliceous spicula.

The author pointed out the importance of this creature as connecting the *Spongiæ Gregarinidæ* and *Polythalamata.*

XIII

REPORT UPON THE RESEARCHES OF PROF. MÜLLER INTO THE ANATOMY AND DEVELOPMENT OF THE ECHINODERMS.

Annals and Magazine of Natural History, ser ii. vol. viii., 1851, *pp.* 1–19

1. Müller, Johann. Ueber die Larven und die Metamorphose der Ophiuren. *Transactions of the Berlin Academy*, 1846.
2. Müller, Johann. Ueber die Larven und die Metamorphose der Echinodermen. *Ibid.* 1848.
3. Müller, Johann. Ueber die Larven und die Metamorphose der Holothurien und Asterien. *Ibid.* 1849–50.
4. Müller, Johann. Anatomisch Studien über die Echinodermen. *Müller's Archiv*, 1850, Heft. ii.
5. Müller, Johann. Berichtigung und Nachtrag zu den anatomischen Studien über die Echinodermen. *Ibid.* Heft iii.
6. Müller, Johann. Fortsetzung der Untersuchungen über die Metamorphose der Echinodermen. *Ibid.* Heft. v.
7. Müller, Johann. Ueber die Ophiuren-larven des Adriatischen Meeres. *Ibid.* 1851. Heft i.

We purpose in the present article to give some account of the results at which the illustrious author of the works whose titles are prefixed has arrived, in the course of a series of elaborate and patiently conducted researches in one of the most remarkable and most obscure provinces of zoological and physiological science. It is a province, too, in which Professor Müller is at once Columbus and Cortez. The discoverer—he has gleaned all its riches. For it so happens that Sars, the only investigator who preceded him in the study of the development of the Echinoderms, had not the good fortune to meet with instances of the ordinary course of development, but only with a case, exceptional among the Echinoderms, but differing less from the embryogenic phænomena of other animals.

Nor are we indebted to the Professor for a widening of our embryo-

logical knowledge alone. A more exact knowledge of development involved the necessity for, and at the same time furnished the key to, a more accurate idea of the adult structure of the Echinoderms.

The ordinary Echinoderms sufficiently try the patience of the anatomist ; and any one who has ever endeavoured to dissect a Holothuria, must recollect the feeling of despair with which he regarded the knotted, glairy eviscerated mass, which was too often the reward of all his care and caution. Undaunted by the great practical difficulties, however, Prof. Müller has entered into these complementary investigations (which are contained in the fourth and fifth treatises of the foregoing list) ; the errors, difficulties, and contradictions which formerly infested the subject have been cleared up and rectified, and the structure of the Ophiuridæ, Asteridæ, Echinidæ, and Holothuriadæ is now capable of being reduced to broad general propositions. Without by any means claiming for the celebrated Berlin physiologist the merit of discovering facts of organization, due to Tiedemann, to Valentin, to Krohn and others, it yet cannot be denied, that under his hands these facts have first assumed their due importance, and become moulded into a consistent whole. Under his authority, then, without always caring to indicate the original sources of information, we shall give the following summary of some points of the organization of the Ophiuridæ, Asteridæ, Echinidæ, and Holothuriadæ, as preliminary, and indeed necessary, to a proper comprehension of their genetic phænomena.

It is not, however, necessary for our present purpose to enter upon the anatomy of any other systems of organs than the water-vascular system, the blood-vascular system, and the nervous system.

In all the families cited, the fundamental part of these three systems consists of three distinct rings, surrounding the œsophagus ; the blood-vascular ring lies innermost, the water-vascular ring next, the nervous ring outermost.

The *blood-vascular* ring, besides the branches which it gives off, is always connected with two vessels which run along opposite sides of the intestine (*Holothuria*) ; and in Asteridæ and Echinidæ there is a distinct tubular heart which connects the vascular ring round the œsophagus with another vascular ring surrounding the anus, from which branches pass to the ovaria, &c.

Branches are given off from the principal blood-vascular ring towards the ambulacra, and in the Holothuriadæ it appears very probable that these branches accompany and indeed inclose the nerves.

The blood-vascular system is everywhere totally unconnected with the water-vascular system.

The *water-vascular* system, whose real disposition it is of great importance to understand, with reference to embryonic states, lies, it has been said, superficial to the blood-vascular system. It forms a ring, which lies close to the integument of the mouth in the Ophiuridæ and Asteridæ, surrounds the œsophagus at the base of the lantern in Echinidæ, and encircles it beneath and at some distance from the calcareous ring in the Holothuriadæ.

From this ring a series of vesicles, varying in number from four (*Ophiura*) to a hundred (*Cladolabes peruanus*), depend. These are the Polian vesicles; they open into the water-vascular ring, and appear to be in some way connected with the distribution of fluid through the water-vascular system.

Connected also with the circular water-vascular ring is the famous sand-canal, of which one or more are found in all the families enumerated. In most there is only one sand-canal, but in some Asteridæ there are several, and in *Synapta serpentina* there are a great number.

The sand-canal is a membranous tube having calcareous particles imbedded in its parietes, which are sometimes (Holothuriadæ) pierced by distinct apertures.

Now the extremity of the sand-canal may be either adherent to some part of the parietes of the animal, as in Ophiuridæ, Asteridæ, Echinidæ, or it may hang loose in the abdominal cavity, as in the Holothuriadæ. In the former case the spot to which it adheres is either entire (*Ophiura*), or perforated by many apertures which communicate with the interior of the canal (Asteridæ, Echinidæ), in which case it forms the " madreporic plate."

But in all cases it is important to recollect that the sand-canal is nothing more than a part of the water-vascular system in which a calcareous deposit has taken place.

Besides all these appendages the circular water-vessel is connected with five vessels, the water-canals, which supply the tentacles and feet and run down the sides of the body in the ambulacral spaces.

The *nervous ring* is formed by a simple cord without ganglionic enlargements, encircling the œsophagus superficial to the water-vascular ring, and giving off five cords which run with, but superficial to, the water-vascular canals in the ambulacral spaces.

The position of the water-vascular canals and of the nervous cords is apparently different in the Asteridæ from what it is in the Echinidæ inasmuch as in the former these organs are *outside* the bony skeleton

in the latter *inside* it ; but this apparent difference arises only from a difference in the mode of development of the ambulacral plates.

The ambulacral plates in the Asteridæ, *between* which the canals lead from the ampullæ to the feet, are homologous with the ambulacral plates in the Echinidæ *through* which they pass.

But in the Asteridæ the ambulacral plates develope internal processes which unite *above*, or internal to, the water-vascular canals and nerves, while in the Echinidæ the ambulacral plates unite *below* or external to the water-vascular canals and nerves.

In the Echinidæ, the only parts that represent the internal processes of the Asteridæ are the "auriculæ"—arched processes which give attachment to the suspensor muscles of the lantern, and under which the vessels and nerves pass.

In the Ophiuridæ both internal and external processes of the ambulacral plates exist, and the vessels and nerves are contained in a complete bony canal.

In the Holothuriadæ the arrangement of parts is as in the Echinidæ. The ring, composed of ten to fifteen bony pieces, encircling the œsophagus, is not homologous with any part of the skeleton of the Echinidæ, but with the lantern or masticatory apparatus.

Five of these pieces are always either notched (as in the Holothuriadæ) or pierced (as in the Synaptæ) for the passage of the water-vessels and nerves, and these pieces correspond homologically with an equal number of calcareous pieces of the lantern of the Echinidæ (falces of Valentin) which cover in the terminations of the radial water-canals in the circular canal.

Every Echinoderm commences its existence as an oval ciliated body like an infusory animalcule, without organs or distinction of parts.

In some genera, such as *Asteracanthion* and *Echinaster*, it appears from the observations of Sars, Agassiz and Desor, that such a germ as this developes at one part one, three, or four short processes or peduncles, by which it is enabled to adhere to other bodies ; among these Prof. Müller thinks he has discovered an aperture. The remainder of the germ gradually enlarges and assumes the form of a starfish. The feet appear on its under side whence the peduncle or peduncles proceed. The latter become smaller, and eventually appear as mere processes on one side of the mouth of the young starfish, finally vanishing altogether.

Now in these larvæ, their inner structure and the mode in which the disc of the starfish is developed do not appear to have been clearly

made out, so that points of comparison with the embryological phænomena to be described subsequently are wanting. One thing however appears evident, viz. that, as in the other forms, the axis of the starfish is oblique to the axis of the larva from which it proceeds.

The larvæ whose development has been observed by Prof. Müller are widely different.

These larvæ may be reduced to two kinds: 1st, those of the Ophiuridæ and Echinidæ (fig. 1, 2, 3); 2nd, those of the Asteridæ and Holothuriadæ (fig. 4, 5, 6, 7).

1. The larvæ of the Ophiuridæ and Echinidæ are somewhat hemispherical bodies, having one edge of their truncated side prolonged into a single flat and wide process, which carries the mouth and œsophagus.

On the hemispherical portion—not at the extremity, but on the side opposite to that which is prolonged into the wide process—is a circular anus. The œsophagus leads from the mouth, which looks in the same direction as the anus, and opens into a globular stomach placed in the hemispherical portion of the larva; a short intestine runs from this at right angles with the direction of the œsophagus to the anus.

The extremity to which the mouth is turned may be considered anterior, the anal side inferior, and it is this position which the animal has in swimming.[1]

In this general description of the form of the larvæ, however, some most important and characteristic features have been omitted. These are, the calcareous rods which form a sort of internal skeleton or framework, and the ciliated fringe which is the organ of locomotion.

The rods are four, eight, or more in number; they run forwards, diverging from the most convex or posterior portion of the hemispherical part of the larva, and still clothed by the substance of the larva, form processes of a considerable length: some of them pass through the margins of the hemispherical part of the larva, some run through and support the buccal prolongation.[2]

The *ciliated fringe* is a sort of ridge, thickly covered with large cilia (which however do not exhibit the wheel motion), which forms the edge of the flat anterior side of the hemispherical part of the larva and of the buccal prolongation. It therefore passes *above* the mouth and before the anus, completely encircling the body in an oblique manner. It is continued forwards on one side and back on the other,

[1] These determinations of anterior and posterior, &c. are altogether different from those of Prof. Müller. The mode of description adopted by the latter is quite accidental, and we have changed it to make the general homologies more clear.

[2] See the figure given in the 'Annals,' *ante*, vol. xix.

upon the processes of the calcareous rods, and thereby attains a great length and complicated appearance, but fundamentally its relations are such as have been described. In some of these larvæ Professor Müller considers that he has detected, in front of and above the mouth, a rudimentary nervous system, consisting of two little ganglia connected by a commissure, whence branches proceed.[1]

We have described the structure common to all the larvæ of this division; there are certain peculiarities in some, however, which are deserving of notice. Thus in some Echinus-larvæ three long processes containing calcareous rods are developed from the convex posterior extremity of the larva (fig. 3).

In other Echinus-larvæ (fig. 2) these do not exist, but four little prominences, richly ciliated, are developed on the hemispherical portion just where the long processes leave it. These are the "epaulettes" of Müller.

In Ophiurid-larvæ the convex side of the larva bears a circlet of cilia (fig. 1).

2. The second form of larvæ has no internal calcareous skeleton. It falls into two subdivisions: (*a*) the form of the Holothuriadæ, and (*b*) the form of the Asteridæ.

a. These larvæ, the *Auricularia* of Müller (fig. 6 and 7), are at first bean-shaped, convex on the dorsal side, concave on the ventral side. An irregular transverse fissure answers to the hilum of the bean, and in this the mouth is placed. The margins of the fissure are edged by a ciliated fringe exactly similar to that of the former kind of larvæ. The anus opens on the ventral surface of the larva, behind the fringe, the posterior portion of which runs between it and the mouth. The fringe forms a continuous circle, the anterior part of which is bent back to form the anterior margin of the fissure in which the mouth lies.

In the course of its growth the margins of the larva and the corresponding parts of the fringe are thrown into numerous lateral processes which give it a scolloped appearance.

The disposition of the intestine, stomach, &c. is as in the first kind of larvæ.

As the larva increases in size and becomes more elongated in form, the primary fringe becomes replaced by a number of ciliated rings which encircle the now cylindrical body of the larva (fig. 7).

b. The Asterid-larvæ.—The *Bipinnaria* (fig. 4), which is the commoner form of Asterid-larva, closely resembles *Auricularia* in its young condition, except that there is a distinct ciliated circle developed upon the surface of the larva in front of the mouth.

[1] In the Pluteus from Heligoland, but not in other larvæ.

Instead, therefore, of the anterior boundary of the fissure of the mouth being formed as in *Auricularia* by the recurved anterior part of the "ciliated fringe," it is formed by the posterior part of a distinct band of cilia.

It is particularly to be observed that this "band," like the extra band in the Ophiura-larva, does not encircle the body—it is altogether in front of and above the mouth.

The position of the anus is as in *Auricularia*. A variety of the Asterid-larva, described by Prof. Müller under the name of *Tornaria*, resembles this condition of *Bipinnaria*, but subsequently adds a ciliated ring like one of those of *Auricularia*, which encircles the body near the anal end[1] (fig. 5).

Bipinnaria increases greatly in size, attaining the length of an inch or more, chiefly by the increase of the anterior part of the body. This assumes a very extraordinary form, both the "band" and the "fringe" throwing out long processes on each side to the number of half-a-dozen, and at the anterior extremity they form two fin-like expansions placed one above the other.

Another Asterid-larva, *Brachiolaria* (Diag. V. [Plate 12]), resembles *Bipinnaria* in general form, but developes three processes anteriorly between the anterior part of the ciliated "fringe" and the anterior ciliated "band."

These are all the forms of Echinoderm-larvæ enumerated by Prof. Müller. Complicated as they seem to be at first sight, it seems to us that they may all be readily reduced to one very simple hypothetical type ; having an elongated form, traversed by a straight intestine, with the mouth at one extremity and the anus at the other, and girded by a circular ciliated fringe ; just like the larvæ of some Annelids (fig. 9).

Supposing such to be the typical form of the Echinoderm-larva, the specific variations are readily derived from it by simple laws of growth. Let the region before the ciliated fringe be called the *pre-trochal* region, the region behind the fringe be called the *post-trochal* region.

Then the Echinoderm-larvæ would appear to be characterized by a disproportionate development of the dorsal post-trochal region (Diag. I^{a}. [Plate 12]) whereby the anus is thrust downwards, and the dorsal part of the ciliated fringe downwards and forwards ; processes are then developed from the ciliated fringe as previously described.

[1] If Prof. Müller's conjecture, that his "wurmförmige Larve" (Larven und Metamorphose der Holothurien und Asterien, p. 27) is a further stage of development of *Tornaria*, be correct, it ultimately assumes a still more worm-like shape, and more closely resembles a Holothurid-larva.

As in the Annelid-larvæ patches of cilia are frequently developed elsewhere than in the principal circle, *e.g.* on the sides of the body, at the bases of the feet, &c., so in the Echinoderms, ciliated elevations and circles (not encircling the body), and even long processes (*Echinus*, *Brachiolaria*), are developed upon other parts of the body of the larva than the "ciliated fringe."

In the Echini and Ophiuridæ these additional parts are developed in the post-trochal region (Diag. I., II., III. [Plate 12]); in the Asteridæ they are as invariably developed in the pre-trochal region (Diag. IV., V., VI. [Plate 12]).

The ciliated circle of the Ophiurid-larva on the dorsal side of the post-trochal region answers precisely to the ciliated "band" on the dorsal side of the pre-trochal region of the Asterid-larva.

We have ventured here to give a general view of the Echinoderm-larvæ different from that put forth by Prof. Müller himself, who, we would with all deference suggest, loses sight of the real position of the ciliated fringe in its apparent bilaterality. Speaking of the ciliated fringe he says, "We may name this circular ciliated fringe (Wimperschnur), to *distinguish it from such as encircle the body transversely*, the *bilateral ciliated fringe*" (Metam. d. Holothurien u. Asterien, p. 35).

We maintain that this "bilateral" fringe itself does, in truth, encircle the body transversely, however distorted it may have become, and the reader is referred to the diagrams for a demonstration of the truth of this position.

A strong confirmation of this opinion is afforded by the structure of the larva of *Sipunculus* described by Max. Müller (Müll. Archiv, 1850, v.). (Fig. 8.)

In this remarkable larva there is a single even band of strong cilia which encircles the anterior part of the animal, and evidently represents the "ciliated fringe" of the other Echinoderm-larvæ. Except that the intestine is bent upon itself, it agrees precisely with our hypothetical type of the Echinoderm-larva.

The Echinoderm-larva, we repeat, may be considered as an Annelid-larva, which has become distorted by the excessive development of the dorsal part of its post-trochal region.[1]

Out of these larvæ, all of which have a strictly bilateral symmetry,

[1] The only other animals which possess a larva at all resembling that of the Echinoderms and Annelids are certain Trematoda (see Müller, Ueber eine eigenthumliche Wurmlarve aus der Classe d. Turbellarien, Müll. Arch. 1850). Here it would appear that by an excessive development of the pre-trochal region, the ciliated fringe has the concavity of its bend posterior; but the difficulty, from the absence of an anus, of determining the real axis of the body, renders this determination doubtful.

the more or less radiate adult Echinoderms are developed by a process which is a sort of internal gemmation.

Now the result of this process is twofold ; either the new structure ultimately throws off more or less of the larva in which it was developed, or it unites with the larva to form the adult animal, no part being thrown off.

The former is the case in the Ophiuridæ, Echinidæ and Asteridæ, for the most part—the latter in the Holothuriadæ.

The latter process, as the simpler, shall be described first.

A portion of the dorsal integument of the larva becomes as it were thrust inwards (fig. 10) towards one or other side of the stomach, as a tube terminated by an enlarged globular extremity, whose cavity communicates with the exterior and is ciliated internally.

The vesicle which terminates this " internal bud " now sends forth processes so as to form a sort of " rosette," which lies close to and above the stomach.

The " rosette " becomes a circular canal (the circular canal of the water-vascular system), from which cæca are given off anteriorly to form the tentacles, posteriorly to the parietes, in which they become the water-canals.

The former mouth of the larva is obliterated, and a new one is formed in the centre of the circular canal and its tentacular appendages. This is the permanent mouth of the Holothuria, which is therefore *a new structure formed upon the dorsum of the larva.*

In the meanwhile, vesicles, the Vesiculæ Polianæ, are developed from the circular canal, and a deposit of calcareous matter takes place round a portion of the tubular canal, from whose spherical extremity the water-vascular system has been formed. That portion of the tubular canal which lies between the dorsal parietes and the calcareous deposition dies away, and the remainder hangs freely from the circular canal of the water-vascular system as the " sand-canal."

The process in the Echinidæ, Asteridæ, and Ophiuridæ is essentially the same ; only, as in these the old body is to be more or less completely discarded, the development of the water-vascular system is attended, *pari passu*, by that of a mass of cells from which the new body is to be formed.

We cannot do better than adduce in illustration Prof. Müller's description of the development of the Echinoderm in the Asterid-larva *Bipinnaria* (Fortsetzung der Untersuchungen über die Metamorphose d. Echinodermen, Müll. Archiv, 1850).

In larvæ which are not 0·15 of a line in length, the dorsal pore and the tube which proceeds from it are perceptible. It passes into a

longish sac, in which, as in the tube, there is a ciliary motion. The sac lies behind, at the side of the œsophagus (Diag. IX. [Plate 12]).

Soon after the appearance of these parts, a hyaline mass, in which very small cells are imbedded, is seen lying like a mantle upon the dorsal side of the stomach.

The sac becomes developed into a rosette of five cæca, the first foundation of the water-vascular system.

The mantle-like mass curves over and covers in the stomach and foundation of the tentacles like a cap, widely open below. The dorsal pore becomes invested by it, and it extends round the anus; but the œsophagus remains outside it (Diag. XI. [Plate 12]).

A crest or elevation now appears on the mantle-like mass, and runs obliquely over it in a curved line, whose ends become eventually united. It then forms the margin of the starfish.

What lies beneath this thickened margin belongs to the dorsum of the starfish, what lies above it to its ventral surface.

The young starfish now attains a diameter of $\frac{1}{7}$th of a line, becomes slightly pentagonal, and retains only a narrow connexion with the *Bipinnaria*.

The digestive canal, and with it the rosette-like rudiment of the water-vascular system, becomes turned so as to present the latter towards the ventral surface of the starfish, at that point where its mouth is subsequently formed. The tube which connected the rosette with the pore, which is now imbedded in the dorsal surface of the starfish, receives a calcareous deposit and becomes the sand-canal, while the " pore " is converted into the madreporic plate.

The œsophagus of the larva is obliterated, whilst its rectum projects as an anal tube subcentrally from the dorsal surface of the starfish (Diag. XIII. [Plate 12]).

The slightest touch now separates the starfish from the larva in which it was developed; the former sinks to the bottom and creeps by the aid of its newly-developed feet; the latter swims about as before for some time, but eventually perishes.

In the Echinidæ the process is essentially the same. An internal diverticulum of the integument of the larva is formed, but from a somewhat different spot,[1] namely in front of the ciliated

[1] It is remarkable that in the Asterid-larvæ, while the development of accessory ciliary processes, &c. takes place in the pre-trochal dorsal region, the bud of the Echinoderm is developed from the post-trochal region. In the Echinus-larvæ we have just the reverse—the bud is developed from the pre-trochal region ("below the lateral arch of the ciliated band," Müller), while the processes, &c., as we have seen, are developed from the post-trochal region. The Ophiuræ appear to present the same relations as the Echinidæ, though Prof. Müller has not been able to make out the point with certainty.

fringe and on one side. It is connected with a vesicle which lies close against the œsophagus, and from which the water-vascular system is developed.

At this place the shell of the *Echinus* subsequently makes its appearance as a circular disc, which gradually envelopes the stomach, and developes tentacles and spines. A new anus is formed as well as a new œsophagus, in the young sea-urchin.

The development of the Ophiuridæ has not been traced so far back as that of the other groups. The dorsal pore and tube have not been observed; but the development of the "rosette" and its accompanying mass of cells into the Echinoderm takes place as in the Asteridæ.

The observations of Dr. Busch (Müll. Arch. 1849) have shown that the larva of *Comatula* very early assumes the form of the Holothurid-larva with ciliated rings, but its internal structure and the development of the Echinoderm are not understood.

To sum up, in Prof. Müller's words, the variations of the metamorphosis of Echinoderms:—

"1. The change of the bilateral larva into the Echinoderm takes place when the larva yet remains an embryo, and is universally covered with cilia, without a ciliated fringe. A part of the body of the larva takes on the form of the Echinoderm; the rest is absorbed by the latter. (A part of the Asteridæ, *Echinaster*, *Asteracanthion*, Sars.)

"2. The change of the bilateral larva into the Echinoderm takes place when the larva is perfectly organized; that is, possesses digestive organs and a special ciliated fringe. The Echinoderm is constructed within the Pluteus like a picture upon its canvas, a piece of embroidery in its frame, and then takes up into itself the digestive organs of the larva. Hereupon the rest of the larva vanishes[1] (*Ophiura*, *Echinus*), or is thrown off (*Bipinnaria*).

"3. The larva changes twice. The first time it passes out of the bilateral type with lateral ciliated fringe into the radial type, and receives instead of the previous ciliated fringe, new locomotive larval organs, the ciliated rings. Out of this pupa-condition the Echinoderm is developed without any part being cast off (*Holothuria*, some Asteridæ).

"If we call embryonic type the condition in which the animal leaves the egg, and when the internal organs are not yet developed, we have four stages or types—the embryonic type, the larval type, the pupa type, and the Echinoderm type. The animal may pass from

[1] It seems questionable how far the integument of the larva over the Echinoderm can be said to vanish, when it is remembered that the pedicellariæ are developed thereon while the Echinoderm is still quite rudimentary.

either of the first three forms into the Echinoderm, or may run through them all." (Larven u. Metam. d. Holoth. u. Asterien, p. 33.)

Furthermore it may be stated that the nature of the change here called development of the Echinoderm, is, that a process of the integument of the larva grows inwards and lays the foundation of the future water-vascular system, on which the other organs of the Echinoderm, whether nervous, vascular or tegumentary, are in a manner modelled.[1]

It is of very great importance to remember this fact in considering the homologies of the parts of the Echinoderms.

If the larva of the Echinoderm pursued its normal course of development, it is obvious that its nervous system, for instance, would be homologous in form and position with that of other Annulose forms. There would be a ring with cerebral ganglia round the œsophagus and a chain of ganglia proceeding therefrom, if the nervous system were of the type of the Annelids. Or if it resembled that of the Trematoda, there would be an œsophageal ring with two opposite ganglia, from which a cord would proceed on each side of the body. But the nervous system of the adult Echinoderm can be reduced to neither of these types; it consists invariably in the Ophiuridæ, Asteridæ, Echinidæ, and Holothuriadæ, of a circular or pentagonal cord surrounding the œsophagus (*of the Echinoderm*) without distinct ganglia. From this five cords proceed, in a perfectly radiate manner, following the course of the water-canals.

The study of development renders the reason of this discrepancy obvious. The œsophagus of the Echinoderm is not homologous with the œsophagus of the larva, nor with the œsophagus of an Annelid, and therefore the nervous ring of the Echinoderm is not homologous with the nervous ring of the Annelid. Indeed, since the mouth of the Echinoderm answers homologically to an aperture in the dorsal wall of the stomach of the larva, and since the nervous system of the Echinoderm follows exactly in its form the form of the water-vascular system of the Echinoderm, which is essentially a process of the dorsal integument of the larva, we might be tempted to conclude that the nervous system of the Echinoderm is homologous, not with the ordinary ganglionic chain of an Annelid, but with that elaborate system of dorsal-proboscidean nerves which M. Quatrefages has detected and described in the latter.

The fact that these nerves supply eye-spots would indeed present some difficulties in the way of this hypothesis, if this system of nerves

[1] Hitherto we have chiefly quoted Prof. Müller, but for what follows we must be considered alone responsible, unless direct mention be made to the contrary.

in the Annelida is truly stomatogastric. But in the first place it has not been shown so to be; and in the second place, the existence of well organized eyes supplied by nerves from the ordinary ventral ganglia in each segment of *Polyophthalmus*, would lead us to hesitate in drawing any very strict conclusions from position and structure to function, in the nervous system of these animals.[1]

Yet one word upon the bearing of the facts of development now made known, on the affinities of the various groups of Echinoderms.

If we were to arrange the Echinoderms according to the nature of their larvæ, we should have one group formed by the Asteridæ, Holothuriadæ and Crinoideæ (*Comatula*); and another composed of the Ophiuridæ and Echinidæ. And if the acute speculation of Prof. E. Forbes, that the pectinated rhombs of the Cystideæ answer to the "epaulettes" of the Echinus-larva, be correct, then the Cystideæ would, as a sort of permanent form of Echinus-larva, fall into the latter group, in which they would represent the Crinoideæ.

Interesting as are the phænomena presented by the larvæ of the Echinoderms, taken in themselves, as mere facts, they are far more important in their bearing upon one of the most comprehensive and interesting zoological theories of modern times—we refer to the theory of "the alternation of generations." Founded by Chamisso and Eschscholz, extended to a great number of new cases by Steenstrup, and finally reduced to a fixed and definite scientific form under the name of "Parthenogenesis" by the celebrated Hunterian Professor of Comparative Anatomy, this theory has bid fair to unite all the aberrant generative processes of the Invertebrata (those of the Echinoderms among the rest) under its conditions, and to express them in its terms.

The theory may be generally expressed thus:—1. The ovum produces an individual A^1, whose offspring is another individual B dissimilar to A^1. This again may in the same way produce an individual C, and so on. The last of the series only contains generative organs from which ova are formed, and these reproduce an individual A^2 precisely resembling A^1. The species, therefore, is said to be represented by a number of generations of individuals which regularly alternate with one another.

To this Professor Owen adds—

2. That the individuals B, C, D, &c. which intervene between the sexual individuals A^1 and A^2 are always developed from masses of cells which are the immediate and unchanged descendants of the

[1] Again, the eyes of the Acephala are as much supplied from the palleal or visceral ganglion as from the cerebral ganglion.

embryo cells of the ovum, and which as such, retain a portion of the original "spermatic force," whence they are enabled to attain a certain independent development without a renewal of the spermatic influence.

Now the questions to be decided before the alternation theory can be said to apply to the Echinoderms or any other animals, are different as regards the two portions of the theory. The problem as regards the first question is a matter of naming—as regards the second it is a matter of fact.

We have said that the question involved in the first part of the theory is a question of naming. It is, whether we can apply to A, B, C, &c. in the foregoing instance, the name "individual." For it is quite clear that if they cannot with propriety be called "individuals," their succession cannot be called an "alternation of generations," inasmuch as generations are composed of individuals.

We must carefully bear in mind that this inquiry has nothing to do with the thorny problem of psychical individuality. With that the zoologist has no concern ; his science investigates the laws of animal form, and in psychological questions he has no more *direct* interest than the astronomer has in the zoology of the planet Saturn.

Leaving psychological considerations aside, then, and inquiring into the *zoological* meaning of the term "individual," we find that anything to which it is applied among the higher and the greater part of the lower animals, has two principal characters : first, it has an independent existence ; and secondly, it is the total result of the independent development of a single ovum.

Now the forms A, B, C, described as "individuals" by Steenstrup, have only one of these characters (in the most strongly marked cases of "alternation"), that of independent existence ; for each of them is only *part* of "the total result of the development of a single ovum."

But in predicating "individuality" of any animal which does not "alternate," we predicate both these characters of it.

Hence, unless the meaning of the term "individual" be altered, the advocates of the alternation theory commit the capital error of using the same term in two very different senses, according as they speak of a Hydra or a Campanularia, a Salpa or a Cynthia.

It is only by narrowing the meaning of the word "individual" to mere "independent existence," that it can possibly become applicable in Steenstrup's sense. But in this case spermatozoa, spermatophora, and even cancer cells, would equally be "individuals." So that the new meaning would be not only entirely arbitrary, but opposed to the general sense of zoologists.

We propose on the other hand not to alter the ordinary zoological meaning of the word "individuality," but merely to define it more strictly, and give to it the relative value of the attributes which it connotes, and which are conversely a mark of it.

Individuality has so long and so obviously, among the higher animals, been observed to be accompanied by independent existence, that the latter attribute has come to be considered as, conversely, an indication of individuality—to the neglect of the really characteristic attribute, which is—the circumstance of being the total result of the development of a single ovum.

According to our view, then, the zoological individual = the total result of the development of a single ovum, whether this total result consist of one or many independent existences. The individual is the zoological unit, and its value is the same, whether we have it as (1) or as $(\frac{1}{3} + \frac{1}{3} + \frac{1}{3})$. A fraction does not become equal to the unit by standing alone. The Cyanæa and the Polype from which it proceeds, the two forms of Salpæ, the parent nurses, nurses, and Cercariæ, of the Distomata, are not distinct individuals—are not separately equivalent to an individual beetle or dog.

It is their sum only which is equivalent to the individual among the higher animals.

They are not the individual, but are successive forms by which the individual is manifested ; standing in the same relation to the individual, as the incarnations of Vishnu to Vishnu, in the Hindoo theology.

What then may these independently existing "parts of individuals" be properly termed ? They can hardly be called organs without doing violence to our ordinary acceptation of the nature of an organ, in which a certain subserviency and dependence is understood. The term "*zooid*" has been devised ; and as it has no theoretical meaning, but is merely intended to suggest two indisputable facts with regard to the creatures to which it is applied—namely that they are like individuals, and yet are not individuals, in the sense that one of the higher animals is an individual—its use does not appear to be open to any serious objection.

Instead of saying then, that in a given species, there is an alternation of so many generations, we should say that the individual consists of so many zooids.

Again, where no "alternation" takes place, the individual = the sum of its organs ; where there is alternation, the individual = the sum of its "zooids."

If the view we have taken be correct, the whole doctrine of the

so-called "compound animals" must be revised, and their terminology altered. A whole tree of Sertularia, a Pennatula, a Pyrosoma, a mass of Botrylli, must no longer be considered as an aggregation of individuals, but as an individual developed into many zooids.

And if the term "compound animal" is to be retained in its old meaning, we know of only one creature which is entitled to the name, viz. the *Diplozoon paradoxum*, which Von Siebold has just shown to be really formed by the fusion of two previously distinct individuals.

We hope that the reader will pardon this long digression into the regions of abstract thought. Whether he adopt our view or not, we trust that at any rate, we have pointed out where the real battle of the alternation theory lies.

The onus of giving a new meaning to the word "individuality" must rest with the advocates of the alternation theory; we have endeavoured merely to make a consistent extension of the old meaning to embrace new facts.

The Echinoderms have been included under the "Alternation theory"; but, if the reasoning above be correct, unjustly, as is indeed plainly pointed out on other grounds by Prof. Müller in his second memoir. He justly observes that the process of development of the Echinoderm partakes as much of the nature of metamorphosis as of "alternation." The larva and the Echinoderm cannot be said to be two individuals, when they possess the same intestine.

Nor, as to the question of fact, does the development of the Echinoderm appear to be a case of "Parthenogenesis."

The structure of the integument of the larva, at the place where the tubular rudiment of the Echinoderm is subsequently formed, is quite undistinguishable from that of any other spot. There are here no descendants of the embryo-cells specially set aside to become developed into the new structure.[1]

The development of the Echinoderm is then neither a process of "alternation of generations" nor of "Parthenogenesis," but the individual consists of two zooids—a larva-zooid and an Echinoderm-zooid, the latter of which is developed from the former by a process of internal gemmation.[2]

[1] The elongated cellular masses which exist on each side of the digestive canal in the larvæ, are very possibly the immediate descendants of the embryo-cells. But Prof. Müller leaves it very doubtful, whether these masses have anything to do with the development of the Echinoderm. Certainly they are not concerned in the development of one most important part of it—the water-vascular system. See Müll. Arch. 1850, p. 466. *Ibid.* 1851, p. 4.

[2] According to Prof. Müller (Archiv, 1851, p. 18) the development of the Echinoderm

The development of the Echinoderms is, as Prof. Müller observes, exactly intermediate between the ordinary process of metamorphosis by ecdysis in insects and the so-called "alternation" of the Trematoda and Aphides.

The phænomena of alternation, or as we have called it, "zooid development," takes place in two ways—by external gemmation and by internal gemmation.

The former process is confined to the Polypes and Ascidians, which form a series leading from the lowest Radiate to the Molluscous types. The latter process on the other hand is restricted to the Worms and Echinoderms, which form a series leading from the lowest Radiate to the Annulose types.

Now in each series three modifications may be detected. The deutero-zooid is developed either—1. from a complete segment of the protozooid, when it is difficult to say whether the process is one of internal or external gemmation ; or 2. from a small portion of a segment, including a portion of the digestive canal ; or 3, from a small portion of a segment, an entirely new digestive canal being formed.

The following table will illustrate the relations of these modifications to one another :—

Zooid Development by

	External Gemmation.	*Internal Gemmation.*
3.	Salpa	Aphides. Trematoda.
2.	Campanularia, Corynidæ, &c.	Echinodermata.
1.	Cyanæa.	Tænia. Nais.

We have hitherto considered the various zooids of each form to be complementary to one another, and all necessary to the perfect manifestation of the individual.

But the law of "irrelative repetition" long since established elsewhere by Prof. Owen, is illustrated here in the development of zooid forms where they are not necessary to the manifestation of the individual.

can only "figuratively" (bildlich) be compared to gemmation, inasmuch as the "formative mass" arises independently.

But since he says immediately afterwards that "the rudiment of the water-vascular system, in general, arises before the rudiment of the parietes of the Echinoderm," and since he shows elsewhere that the origin of the water-vascular system is by the development of a bud-like process inwards—the process may, we think, be called gemmation in much more han a figurative sense.

In the Echinoderm there is one larval-zooid and one Echinoderm-zooid—the "individual" would be incomplete without either.

But in the Cyanæa the single Scyphistoma-zooid developes perhaps twenty Cyanæa-zooids, any one of which would have been sufficient to complete the individual.

The development of the hundreds of polypes of a Sertularian appears to be referable to a similar law. Nay, the "generation by gemmation" of a Hydra or a simple Ascidian, and the fission of a Microstomum, seem, strictly speaking, to be phænomena of the same kind.

As in these cases, however, it is impossible when once the gemma is separated from the parent stock to distinguish it from a true individual, it may seem pedantic and unnecessary to insist upon the distinction.

In concluding, we cannot refrain from remarking upon one character of Professor Müller's researches, of which our imperfect notice can give no idea,—it is the singular candour and philosophic impartiality of the writer. In the course of five years, much that seemed probable at first, had, later, to be rejected—much that seemed certain, to be overthrown. It was often necessary to make pretty hypotheses give way before stubborn facts—to re-examine conclusions that had seemed unquestionable.

If any one be curious to know how this has been done, and desire at the same time to learn in what spirit scientific investigation should be conducted, we cannot do better than refer him to the works whose titles head this Report—they are models.

EXPLANATION OF PLATE I. [Plate 12]

The figures numbered with the Arabic numerals all represent really existing forms, and are taken, with the exception of figures 8 and 9, from Professor Müller's memoirs. The "calcareous rods" are omitted for the sake of clearness.

The figures numbered with the Roman numerals on the other hand are all to be considered merely as diagrams. They represent what the Echinoderm-larvæ would be, if they were, as it were, straightened out and reduced to their simplest elements.

Fig. I.[a] is given in order to show how a symmetrical Annelid-like larva, fig. I., may by development of some of its parts at the expense of others become converted into the Ophiura-larva, fig. I.

Fig. 1. Ophiura-larva	I.	The corresponding diagram.
Fig. 2. Echinus-larva with "epaulettes"	II.	Ditto.
Fig. 3. Echinus-larva with spines viewed from behind	III.	Ditto.
Fig. 4. Asterias - larva (*Bipinnaria*), very young	IV.	Ditto.
Brachiolaria, an Asterias-larva.........	V.	The diagram only is given

[PLATE XII.] *Ann. & Mag. Nat. Hist. S. 2. Vol. 8. Pl. I.*

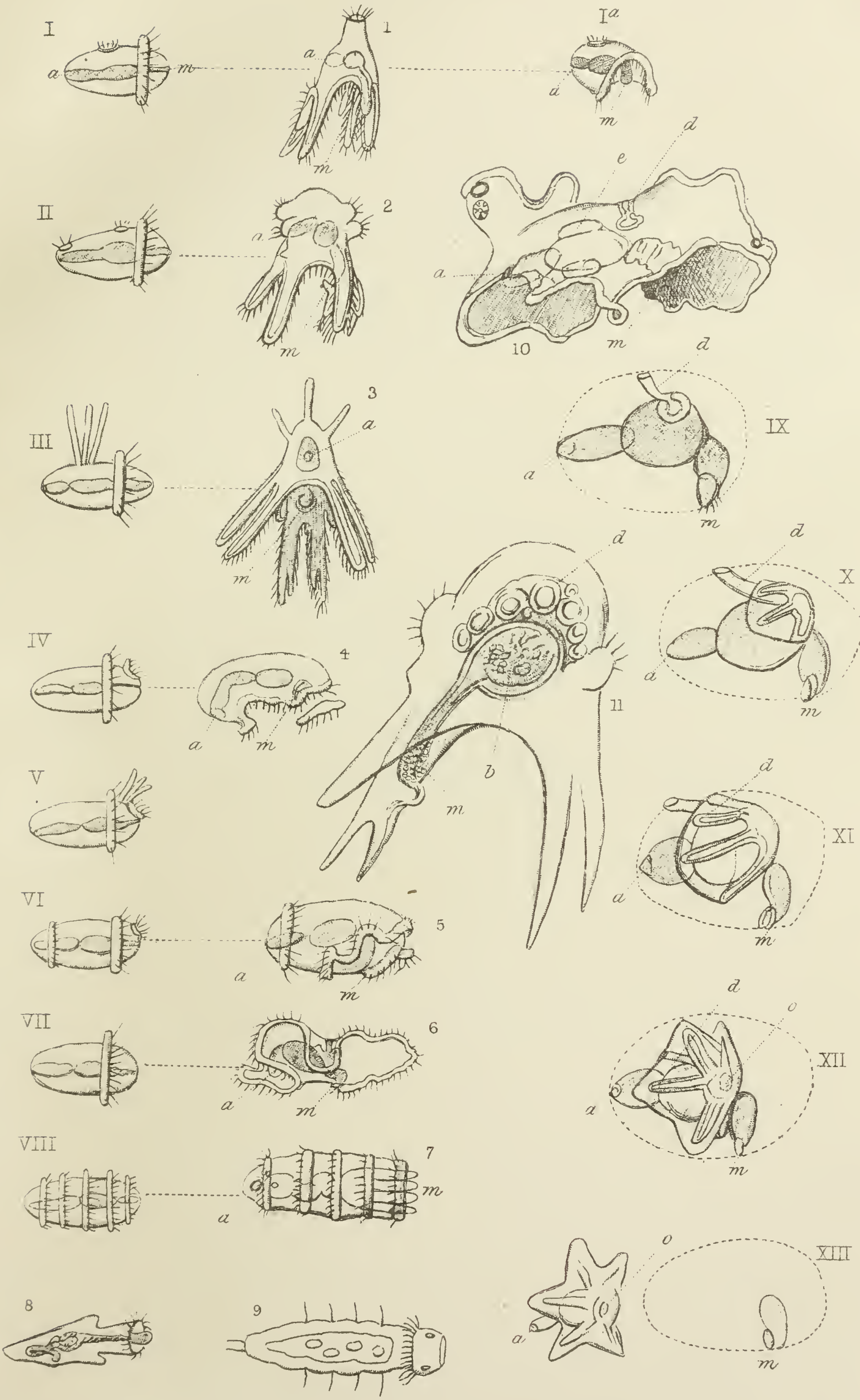

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Fig. 5. *Tornaria*, probably and Asterias-larva	VI.	The corresponding diagram.
Fig. 6. *Auricularia*, the Holothuria-larva in	VII.	Ditto.
Fig. 7. its two forms	VIII.	

In all the figures of larvæ the mouth and anus are indicated by the letters *m* and *a*, and the cilia are disproportionately large so as to render the "fringes" and "bands" evident.

The Diagram No. I. is similarly lettered, and all the other diagrams have their anterior and posterior extremities in a position corresponding to it.

Fig. 8 is the larva of *Sipunculus* after Max. Müller.

Fig. 9. The larva of an Annelid after Milne-Edwards.

Fig. 10. *Auricularia.* The larva of Holothuria, after Müller ; to show the mode of development of the water-vascular system, &c. from the internal bud, *d: e*, the oval masses of cells.

Fig. 11. One of the epauletted Echinus-larvæ, in which the Echinoderm, *d*, has already begun to envelope the stomach of the larva.

IX. X. XI. XII. XIII. are diagrams intended to represent the mode of development of an Asterias within its larva, the *Bipinnaria.*

The form of the latter is not given ; its relation being indicated only by the dotted line.

IX. *m*, the mouth of the larva ; *a*, its anus ; *d*, the bud-like commencement of the Echinoderm.

X. XI. The latter has developed the water-canals, and with its accompanying blastema has begun to invest the stomach of the larva.

XII. The investment nearly complete. The position of the mouth of the Asterias indicated by (*o*).

XIII. The Echinoderm has become free and separate from the body of the larva with its primitive œsophagus.

It is to be understood that these diagrams do not pretend to be strictly accurate. They are intended only to render the process of development more easily comprehensible.

XIV

UEBER DIE SEXUALORGANE DER DIPHYDAE UND PHYSOPHORIDAE.

(Hierzu Taf. XVII. [Plate 13])

Müller's Archiv für Anatomie, Physiologie, und Wissenschaftliche Medicin, 1851, *pp.* 380–4

IN allen Diphyden, soweit ich es beobachtet habe (z. B. *Diphyes*, *Calpe*, *Abyla*, *Eudoxia*, *Aglaisma*, *Cuboides*, *Enneagonum* etc.), ist das Generationsorgan ein medusenförmiger Körper wie bei gewissen Corynidae—und besteht aus einer glockenförmigen Höhle, an der vier auseinanderstrahlende Canäle vorbeigehen, welche an der Peripherie durch einen Randkanal vereinigt werden. Der innere Rand der Glocke ist mit einer circulären Klappenmembran, wie bei vielen Medusen versehen—aber es finden sich weder Tentakel, noch gefärbte Flecke oder Bläschen.

Vor dem Centrum der Glocke hängt ein birnförmiger Sack, wie der Magen einer Meduse, herab. Er ist jedoch an seiner Spitze nicht offen, und die Generations-Elemente, entweder Eier oder Spermatozoen, werden innerhalb seiner Wände entwickelt. Die ovale Höhle innerhalb des Sackes ist reich bewimpert, und communicirt frei mit dem Kanalsystem und (so lange das Organ in Verbindung mit der *Diphyes* steht) mit der allgemeinen Höhle des Polypen oder Polypensystems.

Die monogastrischen Diphyen entwickeln nur die eine Art von Generationsorgan, und alle Polypen einer polygastrischen *Diphyes* auch nur eine Art—so dass die Diphydae sicher getrennten Geschlechts (unisexual) sind.

Die Art der Entwickelung der Generationsorgane ist folgende: beiden Membranen, aus denen der Körper der *Diphyes* zusammengesetzt ist, bilden eine kleine papillare Hervorragung, der Anheftungsstelle der Greiforgane gegenüber. Diese Hervorragung enthält eine Höhle, die bewimpert ist, wie die andern Höhlen dieser Thiere, und frei mit ihnen communicirt.

Das äusserste Ende dieses Forsatzes verdickt sich nun so, dass eine

kleine runde Masse in die Höhle vorspringt, und sie becherförmig macht. So wie die Entwickelung fortschreitet, befestigt sich diese rundliche Masse an vier Punkten, an die Wände der Höhle, so dass sie die becherförmige Höhle in vier Kanälen hinaufzieht.

Die vier Kanäle erweitern sich gelegentlich an ihren Enden und vereinigen sich in einen Cirkelkanal.

Unterdessen ist der Centraltheil der rundlichen Masse durch eine Cavität ausgehöhlt worden, und zwischen den dicken Wänden dieser Cavität und dem Theil des Organs, welcher die Kanäle enthält, ist eine Trennungslinie erschienen, so dass der ganze Bau in eine centrale Portion und eine äussere Höhle getheilt wird. Es zeigt sich nun am Ende der letzteren eine kreisförmige Oeffnung, und das Organ nimmt allmählig seine vollkommene Gestalt an.

Die äussere Wand des centralen Theils ist von Anfang an viel dicker als die innere; in ihr werden die Eier oder Spermatozoen entwickelt. Die ersteren lassen sich zuerst unterscheiden durch das Erscheinen der Keimbläschen und der Keimflecke, um welche die Elemente der Dotter sich allmählig anhäufen.

Wenn sich andererseits Spermatozoen bilden sollen, so findet man, dass die äussere Wand aus blassen kreisförmigen Zellen besteht, welche allmählig einen sehr langen und zarten Schwanz entwickeln, und sich in die verlängerten und zugespitzten röthlichen Köpfe der vollkommenen Spermatozoen verwandt.

In der Mehrzahl der Fälle möchte es scheinen, dass die Generationsprodukte entladen werden, während das Organ noch dem Thiere anhängt, aber in einem neuen Genus (*Sphenia, mihi*) in grosser Menge in der Bussstrasse gefangen, werden die Generationsorgane losgelöst, und schwimmen wie Medusen umher, ehe die Generationsprodukte ihre volle Reife erlangt haben.

In den Physophoriden ist die Natur der Generationsorgane sehr verschieden, je nachdem der zuerst beschriebene Entwickelungsvorgang (der als typischer für beide Gruppen betrachtet werden kann) in einem früheren Stadium aufgehalten oder weiter fortgeführt ist.

In *Stephanomia* und *Athorybia* sind die männlichen Organe denen der Diphyden aber ähnlich, aber die weiblichen Organe sind in ihrer Entwickelung aufgehalten. Sie enthalten nur ein einziges Ei, welches das ganze Innere des Organs einnimmt, das, wenn auch die Kanäle theilweise entwickelt sein mögen, sich nicht in einen centralen Sack und eine äussere offene Höhle trennt.

Die Höhle öffnet sich nicht an ihrem Ende, und muss daher entweder mit dem Ei abfallen oder unregelmässig zerreissen.

In *Physalia* andererseits ist es das männliche Organ, welches

aufgehalten wird ; es findet keine Trennung statt zwischen Höhle und Axe, und nur zwei der (normalen) vier Kanäle sind gebildet ; aber das weibliche Organ wird noch mehr medusenförmig, und, wie es bei einigen Coryniden der Fall ist, scheint seinen centralen Ei- oder samentragenden Sack nicht zu entwickeln, bevor es den gemeinsamen Stamm verlässt. In *Velella* und *Porpita* findet dieses bei den Organen beider Geschlechter statt, wenigstens bin ich niemals irgend einer Form von Generationsorgan in diesen Gattungen begegnet, als solcher, welche zu einem freien medusenförmigen Körper entwickelt wurde (Fig. 16), von dem sich nur, nachdem er frei wurde, ein centraler Sack entwickelte.

Die Physophoriden sind alle hermaphroditisch. In einigen Gattungen, wie *Stephanomia*, werden die Organe der beiden Geschlechter auf verschiedenen Stielen getragen (Fig. 17), in andern, wie *Athorybia*, *Physalia* etc. werden sie auf demselben Stiel getragen.

Ich schlage vor, aus Gründen, die anderswo zu geben sind, Hydroiden und Sertulariden, Polypen—die Diphyden, Physophoriden und Medusiden, in eine grosse Familie zu gruppiren, welche durch viele und auffallende Eigenthümlichkeiten der Organisation charakterisirt ist ; und es ist sehr merkwürdig, zu beobachten, wie die untergeordneten Gruppen dieser Familie einander in den Modificationen, welchen ihre Generationsorgane unterworfen sind, entsprechen, in folgender Weise :

	Generationsorgan aus einem einfachen Fortsatze der Polypenwand gebildet.	Generationsorgan, frei und medusenförmig.
Hydroidae.	*Hydra.*	*Stauridium.*
	Coryne squamata.	(Dujardin.)
Sertularidae.	*Plumularia.*	*Campanularia.*
Diphydae.	?	*Sphenia.*
Physophoridae.	*Physalia.* Männl. Org.	*Velella.*
Medusidae.	*Thaumantiae.*	*Sarsia.*
	Geryonia.	*Lizzia.*

ERKLÄRUNG DER ABBILDUNGEN.

Fig. 1. *Eudoxia.*
a Kernstück ; b Schwimmstück ; c Generationsorgan ; d Magen oder Polyp ; die Greiforgane sind fortgelassen.

Fig. 2. Generationsorgan in seiner jüngsten Form.

Fig. 2 b. Diagromm eines einzelnen Polypen einer *Diphyes.*
a Bractea ; b Stiel des Magens c ; d rudimentäres Generationsorgan.

Fig. 3. Rudimentäres Generationsorgan, in welchem die innere Membran verdickt ist, so dass sie die Höhle becherförmig macht.

[PLATE XIII]

Müller's Archiv 1851

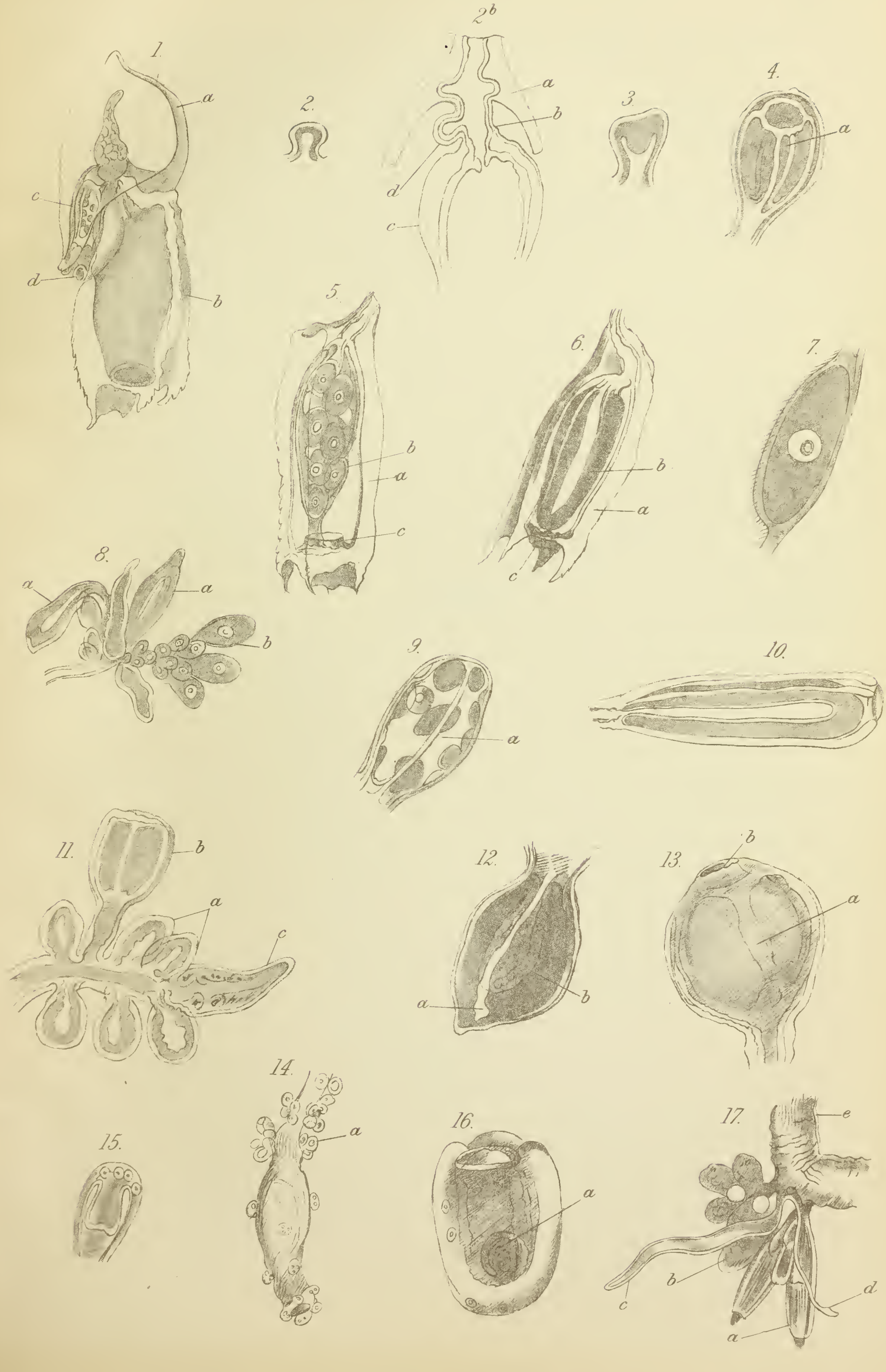


Fig. 4. Dasselbe Organ weiter fortgeschritten; zeigt die vier radialen und den circulären Kanal, nebst der Höhle der centralen Masse a.
Fig. 5. Ein vollständig entwickeltes weibliches Organ.
Fig. 6. Ein vollständig entwickeltes männliches Organ.
In diesen beiden Figuren: a die äussere Höhle mit ihren Kanälen, b der Centralsack, c die klappenförmige Randmembran.
Fig. 7. Ein einzelnes Ei.
Fig. 8. *Athorybia*, ein Bündel von Generationsorganen, a männliche, b weibliche.
Fig. 9. Ein einzeles Ovarium, ein einzelnes Ei enthaltend. Dieses ist theilweise von der umhüllenden Höhle getrennt worden, so dass die Erscheinung von weiten anastomosirenden Kanälen a hervorgebracht wird.
Fig. 10. Männliches Organ.
Fig. 11. *Physalia*, ein Bündel von Generationsorganen a männliche Organe, b weibliche, c ein Magen.
Fig. 12. Ein einzelner Testikel, a Kanal, b Masse junger Spermatozoen.
Fig. 13. Weibliches Organ, a Kanäle, b Oeffnung.
Fig. 14. *Velella*. Einer der kleinen seitlichen polypenähnlichen Magen, welcher die Generationsorgane a trägt.
Fig. 15. Ein junges Generationsorgan mit Fig. 3. zu vergleichen.
Fig. 16. Ein Generationsorgan, welches ein frei schwimmender medusenförmiger Körper geworden ist, a centraler Sack.
Fig. 17. *Stephanomia*. a Männliches Organ, b Ovarien, c ein junger Magen mit seinem Greiforgan d, e das gemeinschaftliche Stamm.

XV

LACINULARIA SOCIALIS.

A CONTRIBUTION TO THE ANATOMY AND PHYSIOLOGY OF THE ROTIFERA

Transactions of the Microscopical Society of London, new series, vol. i. 1853, *pp.* 1–19. (*Read December* 31, 1851)

THE leaves of the *Ceratophyllum*, which abounds in the river Medway, a little above Farleigh Bridge, are beset with small transparent, gelatinous-looking, globular bodies, about 1-5th of an inch in diameter. These are aggregations of a very singular and beautiful Rotifer, the *Lacinularia socialis* of Ehrenberg. On account of their relatively large size, their transparency, and their fixity, they present especial advantages for microscopic observation; and I therefore gladly availed myself of a short stay in that part of the country to inquire somewhat minutely into their structure, in the hope of being able to throw some light on the many doubtful or disputed points of the organization of the class to which they belong.

We are told by Ehrenberg ('Infusions-Thierchen,' p. 403) that *Lacinularia socialis* was discovered and described anonymously in Berlin in 1753. Müller bestowed upon it the name of *Vorticella socialis*, which was changed by Schweigger to *Lacinularia* in 1820. Previously to the time of Ehrenberg the genus appears to have become confounded with *Megalotrocha;* and indeed Dujardin, very reasonably, as it seems, altogether denies the propriety of their separation. The extreme resemblance of the two forms is admitted by Ehrenberg himself; but he considers the attachment of the ova of *Megalotrocha* by a filament to the body—a circumstance which does not obtain in *Lacinularia*—and the existence of a gelatinous investment in the latter which is not found in the former, to be sufficient grounds of distinction.

The matter is not one of much importance, but I call attention to

the close alliance between *Megalotrocha* and *Lacinularia*, for a reason which will appear in the sequel.

The globular aggregations of which I have spoken are not ramified animals like the freshwater Polyzoa, to which, at first sight, they have no small resemblance, but may be truly called compound animals, since each of the *Lacinulariæ* is a separate individual, which at one time swam about freely by itself,[1] which has voluntarily united itself with its fellows, and has taken its share in throwing out the gelatinous substance which connects them into a whole.

Each *Lacinularia* (Pl. I. [Plate 14] fig. 1) has an elongated conical body, whose outer extremity is considerably the wider, and whose inner smaller end is truncated, and serves as a sucker or means of attachment to the stem on which the whole mass is seated; the outer third or fourth of the body contains the viscera, nothing but the muscular cords extending into the inner narrow elongated part of the animal. During contraction, the latter portion is thrown into sharp folds, while the visceral portion presents only three or four faint transverse constrictions.

When the Rotifer is in a state of expansion and activity, its outer extremity is terminated by a large horseshoe-shaped wheel-organ, or "trochal disc" (figs. 2, 3), connected with the body by a narrowed neck. When contracted and at rest, the whole of this apparatus is drawn in, and the body takes on a more pyriform appearance (fig. 5).

The mouth lies in the notch of the trochal disc (fig. 4 *d*); the anus is placed on the opposite side, at the lower part of the visceral portion of the animal (*k*).

Anatomy of Lacinularia.—I will now proceed to describe the various organs of the animal more minutely.

The "trochal disc" is, as I have said, wide and horseshoe-shaped. It is seen in profile at figs. 1 and 2; from above at fig. 3. Its edges are richly beset with large cilia, which present a very beautiful wheel-like movement.

Ehrenberg says that the ciliary organ is "as in *Megalotrocha*," and in this he describes the disc as having a simple ciliated edge. I have not examined *Megalotrocha*, but I can say most decidedly that such is not the structure of *Lacinularia*.[2]

[1] Or rather had the power of swimming about freely; for it does not appear that the young *Lacinulariæ* ever do leave the gelatinous envelope of the parent mass, unless aggregated together.

[2] Leydig (Zur Anatomie und Entwickelungs-geschichte der *Lacinularia socialis*—Siebold and Kölliker's Zeitschrift for February, 1852) says that "an elevated ridge runs along the lower surface of the wheel-organ, not far from, and parallel to, its margin, whence there is a double edge and a groove, in which alone ciliary motion is observed."

In fact, the edge of the disc has a considerable thickness, and presents two always distinct margins—an upper (*p*) and a lower (*p'*), of which the former is the thicker, and extends beyond the latter.

The large cilia are entirely confined to the upper margin, and, seated upon it, they form a continuous horseshoe-shaped band, which, upon the oral side, passes entirely above the mouth (fig. 4). The lower margin (*p'*) is smaller and less defined than the upper, its cilia are fine and small, not more than 1-4th the size of those of the upper margin. On the oral side this lower band of cilia forms a V-shaped loop (fig. 4), which constitutes the lower and lateral margins of the oral aperture. About the middle of this margin, on each side, there is a small prominence, from which a lateral ciliated arch runs upwards into the buccal cavity, and, below, becomes lost in the cilia of the pharynx.

The aperture of the mouth, therefore, lies between the upper and lower ciliary bands. It is vertically elongated, and leads into a buccal cavity with two lateral pouches, which give it an obcordate form: these lateral pouches contain the lateral ciliated arches. A narrow pharynx leads horizontally backwards from the lower part of the buccal cavity, and becomes suddenly widened to enclose the pharyngeal bulb in which the teeth are set. Where buccal cavity meets the pharynx, a sharp line of demarcation exists (fig. 2). In *Melicerta* two curved lines are seen in a corresponding position, and evidently indicate two folds (Pl. II. [Plate 15] fig. 26), projecting upwards into the œsophagus. In *Brachionus* these folds are stronger (fig. 31), while in *Stephanoceros* and *Floscularia* this partition between the œsophagus and what may be called the crop is still more marked. From the inner margin of the aperture in the partition two delicate membranes hang down into the cavity of the crop, which have a wavy motion, and it is to them, I think, that what Mr. Gosse describes as an appearance of "water constantly percolating into the alimentary canal" is due. Dujardin had already noticed (*l.c.*, p. 98) these "vibrating membranes" in *Floscularia* ('Infusoires,' p. 611).

Between the pharyngeal bulb and the mouth there lies on each side of the pharynx a clear, yellowish, horny-looking mass (*f*), which sometimes appears merely cordate, at others, more or less completely composed of two lobes. A similar structure exists in *Brachionus* and *Melicerta*. I believe its function is to give strength to the delicate walls of the pharynx, and that it is therefore to be considered as a part of the horny skeleton.[1]

The general nature of the pharyngeal bulb and of its movements

[1] Leydig (*loc. cit.*) calls these bodies sacs, and considers them to be salivary glands.

has been so often described that it is needless for me to refer to the subject here. With regard to the teeth, however, what I have seen is considerably at variance with the accounts of both Ehrenberg and Dujardin; the former calls the teeth of *Lacinularia* "reihenzähnigen," that is, having a stirrup-like frame, with many teeth set upon it; and the latter, in his general definition of the "Melicertiens," under which head he places *Lacinularia*, has "mâchoires en étrier" ('Hist. Nat. des Infusoires,' p. 612).[1]

As I have seen it (fig. 6), the armature of the pharyngeal bulb in this species—as in *Stephanoceros*—is composed of four separate pieces. Two of these (which form the incus of Mr. Gosse) are elongated triangular prisms,[2] applied together by their flat inner faces; the upper faces are rather concave, while the outer faces are convex, and upon these the other two pieces (the mallei of Mr. Gosse) are articulated. These last are elongated—concave internally, convex externally—and present two clear spaces in their interior; from their inner surface, a thin curved plate projects inwards. At its anterior extremity this plate is brownish, and divided into five or six hard teeth, with slightly enlarged extremities. Posteriorly the divisions become less and less distinct, and the plate takes quite the appearance of the rest of the piece.

This is essentially the same structure as that of the teeth of *Notommata*, described by Mr. Dalrymple ('Phil. Trans.,' 1849), and by Mr. Gosse (on the Anatomy of *Notommata aurita*, Mic. Trans., 1851), and very different from the true "stirrup-shaped" armature.

A narrow œsophagus passes directly downwards from the posterior part of the cavity of the pharyngeal bulb, through the neck of the animal to the body, where it opens into the wide alimentary canal.

This is divided into three portions by an upper, a middle, and a lower constriction.

The two upper parts are often not very distinctly divided. A wide oval or pyriform sac, whose wall contains many nucleated cells, opens into the upper portion on each side. This is the "pancreatic" sac of Ehrenberg.[3]

The middle dilatation frequently gives origin to several short cellular cœca.

The lowest dilatation is globular, and has also several cellular

[1] Leydig also finds Ehrenberg's figures "untrue to nature."

[2] Not described by Leydig.

[3] According to Leydig there are four of these bodies, two smaller and two larger, and they do not open into the alimentary canal.—*Loc. cit.* p. 463.

cœca projecting from its outer surface. Within it is clothed with very long cilia.

The intestine is short and wide, and comparatively delicate; it bends suddenly upwards on the side opposite the mouth, and terminates in a cleft of the integument, whose whole extent it did not seem to me to occupy. (Fig. 1 *k*.)

The Water Vascular System.—This system is thus loosely and confusedly alluded to—I cannot call it described—by Professor Ehrenberg;[1]—"The vascular system consists of transverse circular canals in the body, a vascular network at the base of the wheel-organ, with perhaps a broad circular canal at this part, and of trembling gill-like bodies"—(*loc. cit.* p. 403). The vascular system is so obvious,[2] that it is difficult to understand how it can have been thus blurred over.

The reader will bear in mind that the two bands which run up from the cloaca in many Rotifera, and are usually connected at their extremity with a "contractile vesicle," while they give attachment in their length to the "trembling gill-like organs" of Ehrenberg, are considered by the latter to be the testes. He says that "the trembling organs" appear to be within the sac in *Hydatina*, outside it in *Notommata*.

Von Siebold ('Vergleichende Anatomie') first pointed out that a vessel runs up in each of these bands, and that the "trembling organs" are short branches of these vessels, each of which contains a vibrating ciliary band (Flimmer-läppchen), to which the trembling appearance is due. According to Von Siebold each of these vibrating bodies indicates an opening in the vessel.

Oskar Schmidt ('Versuch einer Darstellung d. Organisation d. Räderthiere'—Erichson's Archiv. 1846) asserts that the ends of the water-vessels are closed, and that the vibrating body is within them.

Dalrymple (*loc. cit.*) saw no testes in the lateral bands of *Notommata*, and considers that the "tags" (the "trembling organs" of Ehrenberg) are externally ciliated at their extremities.

Mr. Gosse ('Microscopical Transactions,' 1851) describes the water-vascular system in *Notommata aurita*, and states that the "tags" of Ehrenberg are really pyriform sacs; but he seems not to have distinguished the contained cilium—at least his description is ambiguous. "When trembling moderately they are seen to be little oval bags attached to the tortuous vessel by a neck and sac at the

[1] "I can thus affirm, that what Ehrenberg describes as vessels in Lacinularia are, in fact, not vessels at all."—*Leydig*, *loc. cit.* p. 463.

[2] Sehr aus-geprägt, Leydig, p. 465.

other end. A spiral vessel, closed at the extremity, runs through most of its length, which maintains a wavy motion"—p. 98.[1]

The following is what I have seen in *Lacinularia*:—There is no contractile sac opening into the cloaca as in other genera; but two very delicate vessels, about 1-4000th of an inch in diameter, clear and colourless (fig. 3 *m*), arise by a common origin upon the dorsal side of the intestine. Whether they open into this, or have a distinct external duct, I cannot say.

The vessels separate, and one runs up on each side of the body towards its oral side (fig. 2). Arrived at the level of the pharyngeal bulb, each vessel divides into three branches (fig. 3); one passes over the pharynx and in front of the pharyngeal bulb, and unites with its fellow of the opposite side, while the other two pass, one inwards and the other outwards, in the space between the two layers of the trochal disc, and there terminate as cœca. Besides these there sometimes seemed to be another branch, just below the pancreatic sacs.

A vibratile body was contained in each of the cœcal branches; and there was one on each side in the transverse connecting branch. Two more were contained in each lateral main trunk, one opposite the pancreatic sacs, and one lower down, making in all five on each side.

Each of these bodies was a long cilium (1-1400th of an inch), attached by one extremity to the side of the vessel, and by the other

[1] M. Udekem (Annales des Sciences, 1851) has given a very elaborate, but I think not altogether correct, account of the water-vascular system of *Lacinularia*. He says that a vascular network exists at the base of the lobes of the wheel-organ; that these unite into gland-like ganglia (my "vacuolar thickenings," in the margin of the disc infra); that from these vessels proceed to the central glands (vacuolar substance, in which the "band" of the water-vascular system terminates, *mihi*), from which three great vessels are given off. Of these, one "passes above the digestive tube, and anastomoses with its fellow from the opposite ganglion; the second presents the same disposition as the first, but is placed below the digestive tube; the third passes directly downwards, skirting the digestive tube"; M. Udekem found it "impossible to trace it any further, but considers that it becomes lost on the digestive canal and ovaries." He, therefore, has missed the external opening of the water-vascular system.

What I have seen and described as "vacuolar thickenings" in the peduncle, are described by M. Udekem as vascular ganglia, from which anastomosing vessels proceed.

As M. Udekem's instrument does not seem to have been good enough to define the vibratile cilium—for he speaks only of a "vibratile or trembling movement"—I venture to think that he has been misled in describing these threads and vacuolar thickenings as forming any part of the true vascular system.

Leydig's opinion of M. Udekem's results is, I find, much the same as my own. He says, "Critically considered, then, we find that Udekem's vascular system in Lacinularia is compounded of a multitude of the most heterogeneous parts of the animal—of structures which belong to the most different systems of organs, without one being a true blood-vessel." —*Loc. cit.* p. 455.

vibrating with a quick undulatory motion in its cavity (fig. 8). As Siebold remarks, it gives rise to an appearance singularly like that of a flickering flame.

I particularly endeavoured to find any appearance of an opening near the vibratile cilium, but never succeeded, and several times I thought I could distinctly observe that no such aperture existed. Animals that have been kept for some days in a limited amount of water are especially fit for these researches. They seem to become, in a manner, dropsical, and the water-vessels partake in the general dilatation.

The "band" (fig. 7) which accompanies the vessel appeared to me to consist merely of contractile substance, and to serve as a mechanical support to the vessel. It terminates above, in a mass of similar substance, containing vacuolæ, attached to the upper plate of the trochal disc. I shall refer to this and similar structures below.

I examined these structures so frequently that I have no doubt that the account I have given is essentially accurate,[1] and I am strengthened in this opinion by the account and figure of the corresponding vessels in *Mesostomum* given by Dr. Max Schulze, in his very beautiful monograph upon the *Turbellaria* (Beiträge zur Naturgeschichte d. Turbellarien). Through these the transition to the richly ciliated water-vessels of the Naidæ, &c., is easy enough.

Vacuolar Thickenings.—(figs. 2, 3 *r*). Under this head I include a series of structures of, as I believe, precisely similar nature, which, on Professor Ehrenberg's principles of interpretation, have done duty as ganglia, testes, &c., in short, have taken the place of any organ that happened to be missing.

In various parts of the body the parietes have become locally thickened, and the prominences thus formed have developed many clear spaces, or vacuolæ—a histological process of very common occurrence among the lower invertebrata.

[1] Leydig's careful description coincides in all essential points with that given above. He particularly notices the fitness of Lacinulariæ that have been imprisoned for some time, for the examination of the water-vascular system.

The only discrepancy of importance in Leydig's account is—firstly, that he considers what I have called the "vacuolar thickening on each side of the pharyngeal mass," and what Ehrenberg calls a nervous centre, to be formed by convolutions of the water-vessel itself; and secondly, that he describes a cloacal vesicle as in other Rotifera. I looked particularly for such a vesicle, but could never see any; in some cases, indeed, I could trace the water-vessels distinct from one another, close to the anus.

Beyond these particular cases, however, I will by no means venture to contradict so accurate an observer as M. Leydig.

Leydig does not seem to have noticed the transverse anastomosing vessel over the pharynx.

Now these thickenings are especially obvious in two localities—1st, in the prolongation of the body below the visceral cavity;[1] and 2ndly, in the trochal disc.

Of the former thickenings, the four uppermost are promoted by Professor Ehrenberg to be testes, for no other reason, apparently, than that, having missed the true water-vascular system with its bands, he knew not where else to find what he calls a male organ.

Again, the thickenings (figs. 2, 3 *r*) in the trochal disc are mostly towards its lower surface and at its inferior margin; they are generally four or five on each side, and are connected by branched filaments with that body on each side of the pharyngeal mass in which the band of the water-vascular system terminates.

According to Professor Ehrenberg these are all ganglia, and the two yellowish bilobed or cordate bodies on each side of the pharynx are "comparable to a brain"!

Nervous System and Organs of Sense.[2]—On the oral side of the neck of the animal, or rather upon the under surface of the trochal disc, just where it joins the neck, and therefore behind and below the mouth, there is a small hemispherical cavity (fig. 4 *o*) (about 1-1400th of an

[1] Leydig (*loc. cit.* pp. 467–8) regards the central vacuolar mass at the root of the tail as a peculiar gland, from which he says a duct runs downwards to terminate at the extremity of the tail. The purpose of this organ is to secrete the gelatinous envelope. I must confess that I saw no grounds for this interpretation. The extremity of the tail always seemed to me to present a ciliated hemispherical cavity, closed above.

[2] Leydig (*loc. cit.* p. 457 *et seq.*) criticises at length, and altogether repudiates, the mythical nerves and ganglions which Professor Ehrenberg has ascribed to *Lacinularia.* He does not appear to have seen either the ciliated cavity, or the body which I still venture to think is the only true ganglion; but describes a very peculiar nervous system, consisting of—

1. A ganglion behind the pharynx, composed of four bipolar cells, with their processes.

2. A ganglion at the beginning of the caudal prolongation, similarly composed of four larger ganglionic cells and their processes.

The latter cells are what I have described as vacuolar thickenings. I could find no difference whatever between them and the thickenings in the disc, which Leydig allows to be mere thickenings.

The former were not observed by me. I have not been able to repeat my investigations upon this point, as I hope to do; for the present I must offer as arguments against Leydig's interpretation of the nature of the structures which he observed—

1st. That the body which I describe as a ganglion is perfectly similar in appearance to the mass on which the eye-spots of *Brachionus* are seated.

2nd. That if such an arrangement of the nervous system as that which Leydig describes exists, the Rotifera are very widely different from their congeners, and, indeed, from all known animals.

Leydig himself, however, says,—"That these cells, with their radiating processes, are ganglion-globules and nerves, is a conclusion drawn simply from the histological constitution of the parts, and from the impossibility of making anything else out of them, unless, indeed, organs are to be named according to our mere will and pleasure."—*Loc. cit.* p. 459.

inch in diameter), which seems to have a thickened wall, and is richly ciliated within. Below this sac, but in contact with it by its upper edge, is a bilobed homogeneous mass (figs. 2 and 4 *n*) (about 1-800th of an inch in diameter), resembling in appearance the ganglion of Brachionus, and running into two prolongations below, but whether these were continued into cords or not I could not make out.

I believe that this is, in fact, the true nervous centre, and that the sac in connection with it is analogous to the ciliated pits on the sides of the head of the Nemertidæ, to the "ciliated sac" of the Ascidians, which is similarly connected with their nervous centre, and to the ciliated sac which forms the olfactory organ of *Amphioxus*.

Mr. Gosse has described a similar organ in *Melicerta ringens*, and I have had an opportunity of verifying his observations, with the exception of one point. According to this observer, the cilia are continuous from the trochal disc into the cup; so far as I have observed, however —and I paid particular attention to the point—the cilia of the cup are wholly distinct from those of the disc.

The interesting observations of the same careful observer upon the architectural habits of *Melicerta* would seem to throw a doubt upon the propriety of ascribing to the organ in question any sensorial function.

But however remarkable it may seem that an animal should build its house with its nose, we must remember that a similar combination of functions is obvious enough in the elephant.

No eye-spots exist in the adult *Lacinularia*. In the young there are two red spots on the upper surface of the trochal disc, which are stated by Professor Ehrenberg to be seated upon "medullary masses" (Mark-Knötchen). I could not satisfy myself either of the truth of this statement or the contrary, in consequence of the difficulty of distinguishing the separate tissues in the young animal.

I may be permitted here to say a word upon the nature of the "calcar," or "respiratory tube," of Ehrenberg, which exists in so many Rotifera. For his first notion, that it is connected with the reproductive system, Professor Ehrenberg has substituted the idea that it is a respiratory tube, through which currents of water are conducted into the cavity of the body, and bathe the "trembling organs" which he calls "gills." Professor Ehrenberg, however, has not produced any evidence of such in-going currents, and Dujardin has denied their existence. So far as has yet been observed, the calcar is in immediate connection with the nervous ganglion. *Melicerta* affords a very good opportunity for examining the structure of the organs, of which in this genus there are two. It is a somewhat conical process of the integnment, containing a similar process of the internal membrane.

This, however, stops short a little distance from the extremity, and forms a transverse diaphragm, from the centre of which a bunch of long and excessively delicate setæ proceeds (fig 29). I could observe no trace of any aperture with a power of 600 diam., though, of course, this is merely negative evidence.

Is it not possible that, as the "ciliated sac" of the Ascidians has its analogue in the "fossa" of the Rotifera, so the calcar may answer to the "languet," which has a similar relation to both sac and ganglion?

In *Notommata* there is no calcar, but nervous cords proceed from the ganglion to the ciliated spots about the middle of the dorsal surface (Dalrymple).

Reproductive Organs.—Considering Professor Ehrenberg's determination of the male organs to be set aside, his description of the reproductive organs extends only to the ovary, which, he says, in *Lacinularia* "lies in the posterior cavity of the body, and has thus one and the same outlet with the intestine" (p. 403). This seems to imply an oviduct; I could, however, see no such organ.[1] The ovary consists of a pale, slightly granular mass of a transversely elongated form (fig. 5 *l*), and somewhat bent round the intestine; it is enclosed within a delicate transparent membrane, which is hardly visible in the unaltered state, but becomes very obvious by the action of acetic acid, which contracts the substance of the ovary, and throws the membrane into sharp folds.

Pale clear spaces, which sometimes seem to be limited by a distinct membrane, are scattered through the substance of the ovary and in each of these a pale, circular nucleus is contained. The nucleus is more or less opaque, but usually contains 1-3 clear spots (fig. 9).

These are the germinal vesicles and spots of the future ova. Acetic acid, in contracting the pale substance, groups it round these vesicles, without, however, breaking it up into separate masses. It renders the nuclei more evident.

The ova are developed thus:—One of the vesicles increases in size, and reddish elementary granules appear in the homogeneous substance round it (fig. 10). This accumulation increases until the ovum stands out from the surface of the ovary, but invested by its membrane, which, as the ovum becomes pinched off as it were, takes the place of a vitellary membrane.

In the meanwhile the germinal vesicle has increased in size and its nucleus is no longer visible. In the ovum it appears as a

[1] Leydig (*loc. cit.* p. 469) says that there is a wide oviduct which becomes folded when empty. I must leave the discrepancy until a further examination decides which is right.

clear space; isolated by crushing the ovum it is a transparent, colourless vesicle.

The perfect ova are oval, about 1-10th inch in diameter, and are extruded by the parent into the gelatinous connecting substance, where they undergo their development (fig. 11).

The changes which take place after extrusion, or even to some extent within the parent, are—1, the disappearance of the germinal vesicle (as I judge from one or two ova in which I could find none); 2, the total division of the yolk, as described by Kölliker in *Megalotrocha*, until the embryo is a mere mass of cells, from which the various organs of the fœtus are developed (figs. 12, 13, 14, 15, 16).

The youngest fœtuses are about 1-70th of an inch in length. The head is abruptly truncated, and separated by a constriction from the body: a sudden narrowing separates the other extremity of the body from the peduncle, which is exceedingly short, and provided with a ciliated cavity, a sort of sucker, at its extremity. The head is nearly circular, seen from above, and presents a central protuberance in which the two eye-spots are situated. The margins of this protuberance are provided with long cilia—it will become the upper circlet of cilia in the adult.

The margin of the head projects beyond this, and is fringed with a circlet of shorter cilia: this is the rudiment of the lower circlet of cilia in the adult. The internal organs are perceived with difficulty; but the three divisions of the alimentary canal, which is as yet straight, and terminates in a transparent cloaca, may be readily made out. The water-vascular canals cannot be seen, but their presence is indicated by the movement of their contained cilia here and there (fig. 17).

In young *Lacinulariæ*, 1-30th of an inch in length, the head has become triangular, the peduncle is much elongated, and thus it gradually takes on the perfect form (fig. 18). The young had previously crept about in the gelatinous investment of the parents; they now begin to "swarm," uniting together by their caudal extremities, and are readily pressed out as united free swimming colonies, resembling, in this state, the genus *Conochilus*.

The process of development of these ova is therefore exactly that which takes place in all fecundated ova, and would lead one to suspect that spermatozoa should be found somewhere or other.

Now, from the observations of Mr. Dalrymple, we should be led to seek a distinct male form with the ordinary spermatozoa. From those of Kölliker, on the other hand, we should equally expect to find

each individual a hermaphrodite, with the very peculiar spermatozoon-like bodies which he has described in *Megalotrocha.*

I must have examined some scores of individuals of Lacinularia with reference to the former case, without ever finding a trace of a male individual. All were similar, all contained either ova or ovarium, nowhere was an ordinary spermatozoon to be seen. On the other hand, I found in many individuals singular bodies, which answered precisely to Kölliker's description of the "spermatozoa" of *Megalotrocha.* They had a pyriform head about 1-1000th in. in diam. (fig. 19), by which they were attached to the parietes of the body, and an appendage four times as long, which underwent the most extraordinary contortions, resembling, however, a vibrating membrane much more than the tail of a spermatozoon; as the undulating motion appeared to take place in only one side of the appendage, which was zigzagged, while the other remained smooth.

According to Kölliker again, these bodies are found only in those animals which possess ova undergoing the process of yolk division, while I found them as frequently in those young forms which had not yet developed ova, but only possessed an ovary.

Are these bodies spermatozoa?[1] Against this view we have the unquestionable separation of the sexes in *Notommata*, and the very great difference between these and the spermatozoa of *Notommata.* Neither are the mode of development nor the changes undergone by the ovum any certain test that it requires or has suffered fecundation, inasmuch as the process closely resembles the original development of the aphides (*see* Leydig, Siebold and Kölliker, Zeitschrift, 1850).

In the view that Kölliker's bodies are true spermatozoa, it might

[1] Leydig (*loc. cit.* p. 474) has observed, in several cases, what I describe as probable spermatozoa, but considers them to be parasites.

He does not notice the similarity of these bodies to those described by Kölliker in *Megalotrocha*; but thinks that the latter has been misled by the vibratile organs.

Leydig does not appear to be acquainted with the important observations of Dalrymple, Brightwick, and Gosse; but brings forward as the true spermatozoon, a *tertium quid*, whose description I subjoin in his own words:—"In almost every colony we meet with from one to four (in large colonies) individuals which are distinguishable from the rest at the first glance. By reflected light they appear quite white, which appearance arises from peculiar corpuscles which fill the cavity of the body more or less completely, and are driven hither and thither by the contractions of the animal, as well as into the wheel-organ as into the caudal appendage. They are yellowish globular bodies, with sharp contours, 1–5000th to 1–1700th of an inch in diameter, with a double centre and a lighter periphery. The surface is covered by a mesh-work of bands projecting internally, which give the body a mosaic (parquettirtes) appearance. Immovable hairs, 1–1700th of an inch long, may be seen in isolated globules to radiate from the surface."

I have not observed any of these bodies.

be said—1. That the sexes are united in most Distomata, for instance, and separated in species closely allied (*e.g. D. Okenii*).

2. That the differences between these bodies and the spermatozoa of *Notommata* is not greater than the difference between those of *Triton* and those of *Rana*.

3. That their development from nucleated cells within the body of *Megalotrocha* (teste Kölliker) is strong evidence as to their having *some* function to perform ; and it is difficult to imagine what that can be if it be not that of spermatozoa. However, it seems to me impossible to come to any definite conclusion upon the subject at present.[1]

Kölliker supposes that Ehrenberg has seen the "spermatozoa," and has taken them for the "long vibratile bodies" ; while Siebold imagines that Kölliker has taken the long vibrating bodies for spermatozoa. No one, however, who has seen both structures can be in any danger of confounding the one with the other.

Asexual propagation of Lacinularia.—Whatever may be the nature of the process of reproduction just described, there exists another among the Rotifera, which has been noticed by almost every one, but not hitherto distinguished or understood. This is the production of the so-called "winter ova," but which from their analogy with what occurs in *Daphnia*, I prefer to call "ephippial ova."

Ehrenberg says that many ova of *Hydatina* have a double shell, and between the two shells there is a wide space. "Similar ones occur in many *Rotifera*, in various often irregular forms : these have a much slower development, and I call them thence winter ova" (p. 413). See also his account of *Brachionus urceolaris* (p. 512). He does not notice the occurrence of these ova in *Lacinularia* or *Megalotrocha*.

Kölliker speaks of the ova of *Megalotrocha* acquiring a deep yellow investment, as if it were a further development of those ova whose yolk he saw divided. I am strongly inclined to believe, however, that he was misled by the peculiar appearance of the winter ova which look as if they had undergone yolk division.

Dalrymple gives a lengthened account of these peculiar ova in *Notommata*. He says that they are dark, and that their outer covering appears to consist of an aggregation of cells, under which is a second layer of cells containing pigment molecules. No distinct germinal vesicle, he says, is to be found in these ova "from the want of general transparency" (*loc. cit.* p. 340).

[1] I may mention here that I have found in *Melicerta* an oval sac lying below the ovary, and containing a number of strongly-refracting particles closely resembling in size and form the heads of the spermatozoa of *Lacinularia*.

It will be observed that all these authors consider the winter ova or ephippial ova and the ordinary ova to be essentially *identical*, only that the former have an outer case. The truth is, that they are essentially *different* structures. The true ova are single cells which have undergone a special development. The ephippial ova are aggregations of cells (in fact, larger or smaller portions—sometimes the whole—of the ovary), which become enveloped in a shell and simulate true ova.

In a fully grown *Lacinularia* which has produced ova, the ovary, or a large portiom of it, begins to assume a blackish tint (fig. 20); the cells with their nuclei undergo no change, but a deposit of strongly refracting elementary granules takes place in the pale connecting substance. Every transition may be traced from deep black portions to unaltered spots of the ovarium, and pressure always renders the cells with their nuclei visible among the granules. The investing membrane of the ovary becomes separated from the dark mass so as to leave a space, and the outer surface of the mass invests itself with a thick reddish membrane (fig. 21), which is tough, elastic, and reticulated from the presence of many minute apertures. This membrane is soluble in both hot nitric acid and caustic potass.[1]

The nuclei and cells, or rather the clear spaces indicating them, are still visible upon pressure, and may be readily seen by bursting the outer coat.

By degrees the ephippial ovum becomes lighter, until at last its colour is reddish brown, like that of the ordinary ova; but its contents are now seen to be divided into two masses—hemispherical from mutual contact (fig. 22). If this body be now crushed, it will be found that an inner structureless membrane exists within the fenestrated membrane, and sends a partition inwards, at the line of demarcation of the two masses (fig. 23). The contents are precisely the same as before, viz., nuclei and elementary granules (fig. 24). This, indeed, may be seen through the shell without crushing the case.

I was unable to trace the development of these ephippial ova any further. Those of *Notommata*, it appears, lasted for some months without change (Dalrymple).

It is remarkable that in Lacinularia these bodies eventually, like the ephippium of *Daphnia*, contain two ovum-like masses; and there

[1] Leydig (*loc. cit.* p. 453) says that the shells of the ova were not dissolved by maceration in a solution of caustic soda (cold ?) for twenty-four hours, and thence concludes that they may be composed of chitin.

The above observation tends to the contrary conclusion.

can, I think, be little doubt that the former, like the latter, are subservient to reproduction.

There are then two kinds of reproductive bodies in *Lacinularia* :—

1. Bodies which resemble true ova in their origin and subsequent development, and which possess only a single vitellary membrane.

2. Bodies, half as large again as the foregoing, which resemble the ephippium of *Daphnia* ; like it have altogether three investments ; and which do not resemble true ova either in their origin or subsequent development ; which, therefore, probably do not require fecundation, and are thence to be considered as a mode of asexual reproduction.[1]

General Relations of the Rotifera.—It is one of the great blessings and rewards of the study of nature that a minute and laborious investigation of any one form tends to throw a light upon the structure of whole classes of beings. It supplies us with a fulcrum whence the whole zoological universe may be moved. I would illustrate this truth by showing how, in my belief, the structure of *Lacinularia*, as thus set forth, taken in conjunction with some other facts, gives us a clue to the solution of the questio vexata of the zoological position of the Rotifera, and thence to the serial affinities of a large portion of the Invertebrata.

The curious analogy in form between the genus *Stephanoceros* and the Polyzoa has, I believe, been the chief consideration which has led many naturalists, both in England and on the Continent, to arrange the Polyzoa and Rotifera together. This has been done in two ways, either by denying the affinity of the Rotifera with the Vermes, and so approximating them to the Polyzoa considered as organized on the molluscous type, or, as Leuckhart has done, by admitting the affinity of the Rotifera with the Vermes, but denying that of the Polyzoa with the Mollusca.

[1] Leydig distinguishes particularly between the ordinary, and what I have termed, the ephippial ova.

His description of the latter agrees essentially with that which has been given above ; but he has not, I think, observed the genesis of the ephippial ova with sufficient care, and he thence interprets their structure by supposing that they are ordinarily fecundated ova, which have undergone a peculiar method of cleavage. The tendency of the observations detailed above, on the other hand, is to show that they are not ova at all in the proper sense, but peculiar buds like those of *Aphis* or *Gyrodactylus*, and as such are capable of development without fecundation.

In the new edition of Pritchard's 'Infusoria,' it is stated (p. 620), that "in a recent paper by Mr. Howard on this species, he states that there are two kinds of reproductive bodies—one the ordinary ova, the other twice their size, representing gemmæ.' No reference is given to Mr. Howard's paper, and I have been at a loss to discover it, though desirous to do justice to him if possible.

I believe that there is a fundamental error in each case, namely, that of approximating the Polyzoa and the Rotifera at all. The resemblance between *Stephanoceros* and a Polyzoon is very superficial. No Polyzoon has the cilia on its tentacles arranged like those of *Stephanoceros*; nor has any a similarly-armed gizzard: still less is there any trace of the water-vascular system which exists in all Rotifera.

The relations between the Polyzoa and the Rotifera, then, are at the best mere analogies.

On the other hand, the general agreement in structure between the Rotifera and the Annuloida—under which term I include the Annelida, the Echinoderms, Trematoda, Turbellaria, and Nematoidea—is very striking, and such as to constitute an unquestionable affinity.[1]

The terms of resemblance are these:—

1. Bands of cilia, resembling and performing the functions of the wheel-organs, are found in Annelid, Echinoderm, and Trematode larvæ.

2. A water-vascular system, essentially similar to that of the Rotifera, is found in Monœcious Annelids, in Trematoda, in *Turbellaria*, in Echinoderms, and, perhaps, in the Nematoidea.[2]

3. A similar condition of the nervous system is found in *Turbellaria*.

4. A somewhat similarly-armed gizzard is found in the Nemertidæ; and the pharyngeal armature of a Nereid larva may well be compared with that of *Albertia*.

5. The intestine undergoes corresponding flexures in the Echinoderm larvæ. There are, therefore, no points of their organization in which the Rotifera differ from the Annuloida; and there is one very characteristic circumstance, the presence of the water-vascular system, in which they agree with them.

Now, with what Annuloida are the Rotifera most closely allied? To determine this point, we must ascertain what is the fundamental type of organization of the Rotifera.

Suppose in *Lacinularia* a line to be drawn from the mouth to the anus, and that this be considered as the axis of the body; suppose, again, that the side on which the ganglion lies is the dorsal side, the opposite being the ventral; suppose, also, the mouth end to be anterior, the anal end posterior,—then it will be found that the lower circlet of cilia upon the trochal disc encircles the axis of the body,

[1] M. Milne-Edwards, with his accustomed acuteness, pointed out (Annales des Sciences, 1845) the close affinity of the Rotifera with the Annelids, the Turbellaria, and the Nematoidea; but he did not include the Echinoderms in the group, doubtless because, at the time he wrote, sufficient was not known of the Echinoderm larvæ to demonstrate their truly annuloid nature.

[2] To these may be added the Cestoidea and the Nemertidæ.

while the upper circlet of large cilia does not encircle the axis, but lies in the lower and anterior region of the body.

If the region behind that ciliary circlet which is traversed by the axis be called the post-trochal region, and that in front of it the pre-trochal region, we find that the circlet of large cilia is developed in the inferior pre-trochal region.

Now compare this Rotifer with the larva of an Annelid. It will be immediately seen that the two are of essentially the same type, only that, while the Annelid larva is equally and symmetrically developed in all its regions, and has frequently no accessory ciliated bands, the Rotifer has its superior post-trochal and inferior pre-trochal regions developed in excess; so that the anus is thrown to the ventral, while the mouth is thrust towards the dorsal surface,[1] an accessory ciliated circlet being at the same time developed in the latter region.

Melicerta ringens (compare figs. 26-28) resembles *Lacinularia* in the arrangement of its ciliated bands, only they are far more distorted from their normal circular form. Tubicolaria closely resembles *Melicerta*, and there can be little doubt that *Megalotrocha* and *Limnias* are to be added to this division.

In *Brachionus*, *Philodina*, *Rotifer*, *Notommata*, the same fundamental type obtains, but the deviation from symmetry takes place in a different way.

In all these it is the ventral post-trochal region which is over-developed, and therefore the anus is thrown to the dorsal or ganglionic side.

In *Notommata* the trocha appears to be simple and unaltered in most species, and there is no accessory circlet.

In *N. aurita*, however, as it appears from Mr. Gosse's description, and in *Brachionus polyacanthus* (figs. 30-33), several processes, three in the latter case, are developed from the superior pre-trochal region. They are richly ciliated, and appear to represent the accessory circlet of *Lacinularia*.

Another distinct type is presented by *Philodina* (figs. 34-37). In this the great trocha is bent upon itself, and the anterior division of it, at first sight, simulates an accessory circlet developed in the superior pre-trochal region. It is not so, however, as the continuity of the band of cilia can be readily traced throughout.

To this division of the Rotifera, viz., those which have the anus on the same side of the body as the ganglion, appear to belong the genera

[1] This over-development is not a mere matter of hypothesis. The young *Lacinularia* has the anus nearly terminal and the "peduncle" only subsequently attains its full proportions. Compare fig. 17 and fig. 18, Pl. I. [Plate 14].

Stephanoceros and *Floscularia*—at least, if the ganglion be what I believe it to be, a granular mass, in connection with the upper part of a large oval mass composed of clear cells, and having a pit in its centre exteriorly, which I believe to be the altered ciliated sac.

These might then be considered as Notommatæ whose trochal circlet had become produced into long processes in *Stephanoceros*, while they remain as shorter knobs in *Floscularia*; a tendency to which development may be traced in the little processes into which the trochal circlet is thrown around the mouths of *Lacinularia* and *Melicerta*, and perhaps in the three processes which, according to Mr. Dalrymple, arch over the mouth in *Notommata*.

But *Stephanoceros*, *Philodina*, *Notommata*, *Brachionus*, and *Lacinularia* are the types of the great divisions of the Rotifera, and whatever is true of them will probably be found to be true of all the Rotifera.

We may say, therefore, that the Rotifera are organized upon the plan of an Annelid larva, which loses its original symmetry by the unequal development of various regions, and especially by that of the principal ciliated circlet or trochal band; and it is curious to remark that, so far as the sexes of the Rotifera can be considered to be made out (approximately), the diœcious forms belong to the latter of the two modifications of the type which have been described, while the monœcious forms belong to the former.

It is this circumstance which seems to me to throw so clear a light upon the position of the Rotifera in the animal series. In a report in which I have endeavoured to harmonise the researches of Prof. Müller upon the Echinoderms,[1] I have shown that the same proposition holds good of the latter in their larval state, and hence I do not hesitate to draw the conclusion (which at first sounds somewhat startling), that *the Rotifera are the permanent forms of Echinoderm larvæ*, and hold the same relation to the Echinoderms that the Hydriform Polypi hold to the Medusæ, or that *Appendicularia* holds to the Ascidians.

The larva of *Sipunculus* might be taken for one of the Rotifera; that of *Ophiura* is essentially similar to *Stephanoceros*; that of *Asterias* resembles *Lacinularia* or *Melicerta*. The pre-trochal processes of the Asterid larva *Brachiolaria* are equivalent to those of *Brachionus*.

Again, the larvæ of some Asterid forms and of *Comatula* are as much articulated as any Rotifera.

It must, I think, have struck all who have studied the Echinoderms, that while their higher forms, such as *Echiurus* and *Sipunculus*, tend clearly towards the Diœcious Annelida, the lower extremity of the series seemed to lead no whither.

[1] Annals of Natural History, 1851.

Now, if the view I have propounded be correct, the Rotifera furnish this wanting link, and connect the Echinoderms with the Nemertidæ and Nematoid worms.

At the same time it helps to justify that breaking up of the class Radiata of Cuvier, which I have ventured to propose elsewhere, by showing that the Rotifera are not "radiate" animals, but present a modification of the Annulose type—belong, in fact, to what I have called the *Annuloida*, and form the lowest step of the Echinoderm division of that sub-kingdom.

From our imperfect knowledge of the Nematoid worms it is difficult to form a definite scheme of the affinities of the Annuloida; but, perhaps, they may be sketched as in the Diagrams, Pl. III. [Plate 16]. These diagrams represent the arrangement of the ciliated bands with relation to the axis of the body in the Rotifera.

Underneath each Rotifer is an Annelid or Echinoderm larva, with its ciliary bands represented in a like diagrammatic manner, to show the essential correspondence between the two.

This paper is now printed exactly as it was read before the Microscopical Society on the 31st of December, 1851, with the exception of those notes which refer to the very excellent memoir of Dr. Leydig, published in February, 1852. Dr. Leydig must have been working at the subject at about the same time as myself, in the autumn of last year; and if I refer to the respective dates of our communications, it is merely for the purpose of giving the weight of independent observation to those points (and they are the most important) in which we agree.

It is the more necessary to draw attention to this fact, since Professor Ehrenberg, in a late communication to the Berlin Academy, hints that the younger observers of the day are in a state of permanent conspiracy against his views. T. H. H.

July 9, 1852.

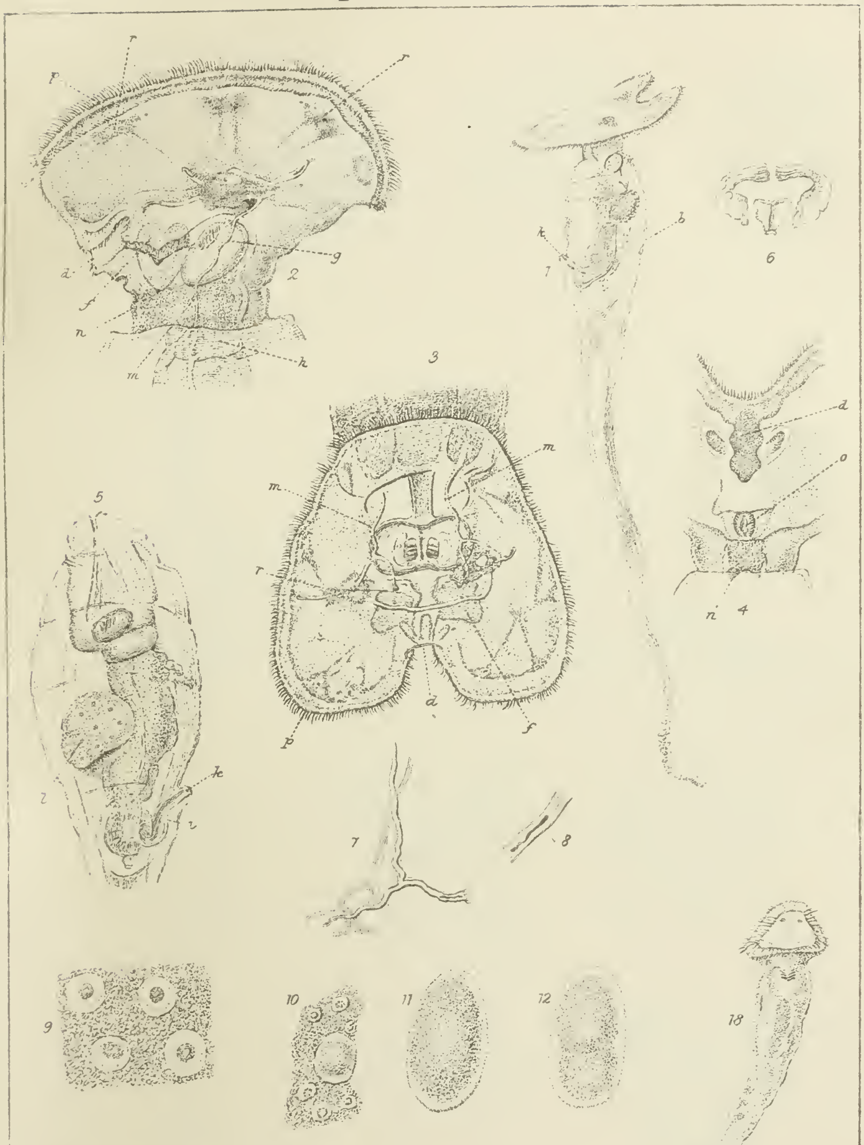
DESCRIPTION OF THE PLATES.

The letters throughout have the same signification :—*a*, trochal disc; *b*, body; *c*, tail of peduncle; *d*, mouth; *e*, pharynx; *f*, "yellow mass"; *g*, gizzard; *h*, "pancreatic sacs"; *i*, rectum; *k*, anus; *l*, ovary; *m*, water-vessels; *n*, ganglion; *o*, ciliated sac; *p*, upper circlet of cilia; *p'*, lower circlet of cilia; *r*, vacuolar thickenings.

PLATE I. [Plate 14].

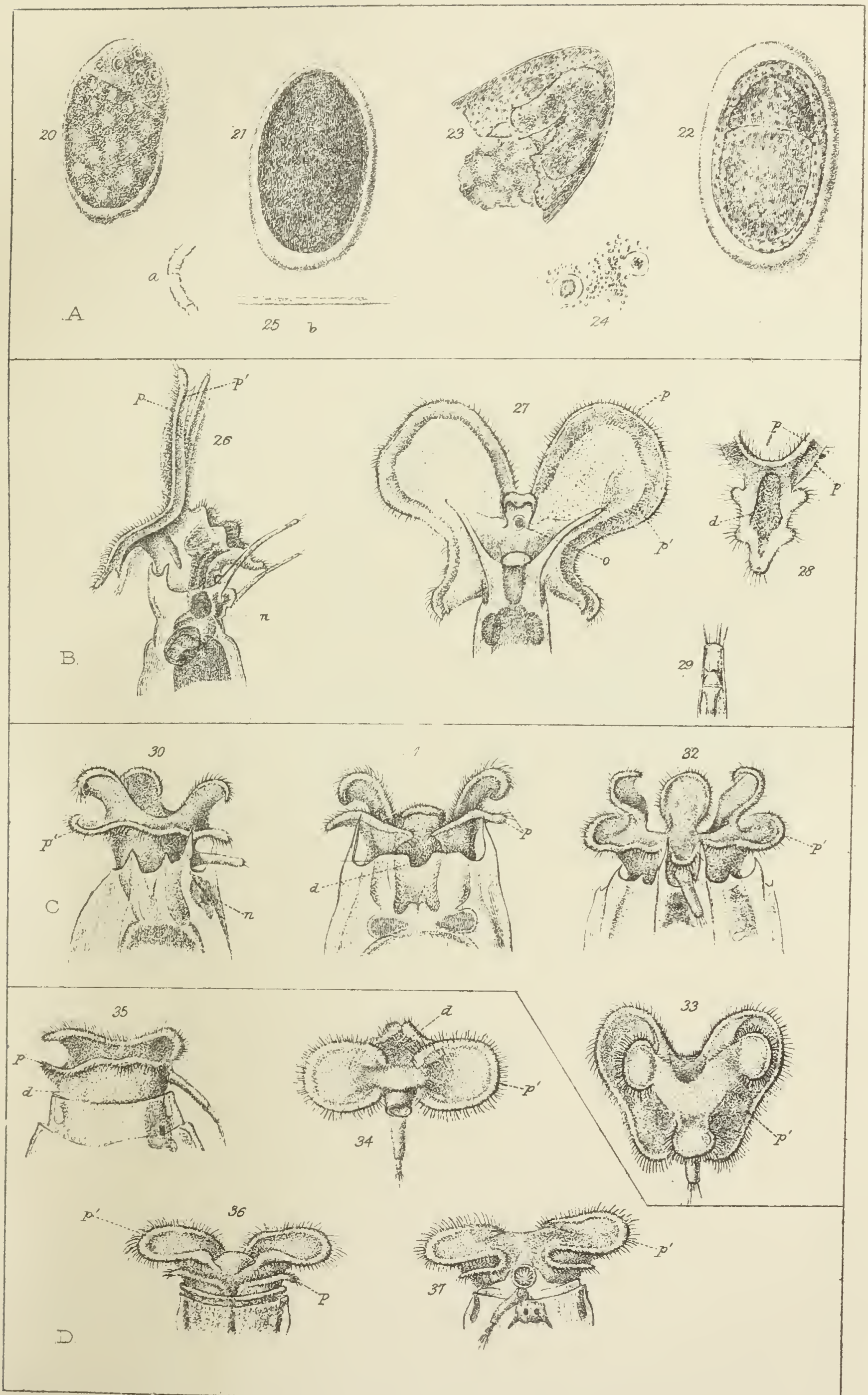
Lacinularia socialis.

FIG.
1. A single individual from the side.
2. Lateral view of the trochal disc.
3. Trochal disc from above.
4. Aperture of the mouth—ciliated sac and ganglion.
5. Animal retracted.



T. Bruey del. Tuffen West, sculp.

LACINULARIA



T. Bradley del. Tuffen West sculp.

A. LACINULARIA B. MELICERTA. C. BRACHIONUS.
D. PHILODINA.

[PLATE XVI.] Trans. Micr. Soc. Pl. III

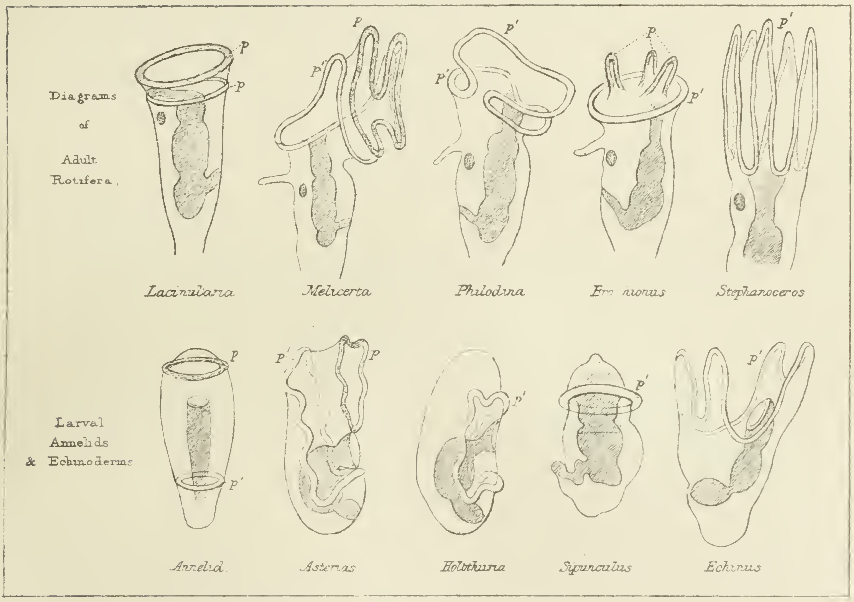


FIG.
6. Armature of the gizzard, viewed laterally.
7. Termination of a water-vessel in the trochal disc.
8. Water-vessel much magnified, showing the long flickering cilium.
9. A portion of the ovary much magnified, showing the germinal vesicles with their spots scattered through its substance.
10, 11. Stages in the growth of the ovum.
12–18. Stages in the development of the embryo.
19. Spermatozoon.

PLATE II. [Plate 15].

20. A portion of the ovary undergoing the change into an ephippial ovum
21, 22. Ephippial ova, the latter having its contents divided into two portions
23. Ephippial ovum burst.
24. Its contents.
25. Muscular fibre—relaxed, *a* ; contracted, *b*.

Melicerta ringens.

26. Viewed laterally.
27. From the ganglionic side.
28. From the mouth side.
29. Extremity of the calcar, showing its apparent closure and the bundle of cilia.

Brachionis polyacanthus.

30. Viewed laterally.
31. From the mouth side.
32. From the ganglionic side.
33. From above.

Philodina, sp. ?

34. Trochal disc from above.
35. ———— laterally.
36. From the mouth side.
37. From the ganglionic side.

PLATE. III. [Plate 16].

The Diagrams illustrate Mr. Huxley's paper of Adult Rotifera, and of Larval Annelids and Echinoderms.

XVI

UPON ANIMAL INDIVIDUALITY

Proceedings of the Royal Institution, vol. i. 1851–4 *pp.* 184–9

(Abstract of a "Friday Evening Discourse," April 30, 1852)

THE Lecturer first briefly described the structure of the Diphydæ and Physophoridæ—pointing out the general conformity of these animals with the common Hydra.

They differ, however, in this important respect; that the body in which the eggs are developed is in Hydra a simple process; while in the Diphydæ and Physophoridæ the corresponding body presents every degree of complication from this form, to that of a free-swimming, independent "Medusa."

Still more striking phenomena were shown to be exhibited by the Salpæ. In this genus each species has two forms. In the example chosen these forms were the S. democratica and the S. mucronata; the former is solitary and never produces ova, but developes a peculiar process, the gemmiferous tube"; upon which, and from which, the associated Salpæ mucronatæ are formed by budding.

Each of these carries a single ovum, from which the first form is again developed.

The Salpa mucronata, which is thus produced from the Salpa democratica, is just as highly organized as the latter. It has as complete a circulatory, nervous, and digestive apparatus, and moves about and feeds as actively; no one unacquainted with its history would dream of its being other than a distinct individual animal, and for such it has hitherto passed.

But the Salpa mucronata has exactly the same relation to the S. democratica that the free-medusiform egg-producing body of Physalia or Velella has to the Physalia or Velella; and this free-medusiform body is homologous with the fixed medusiform body of Diphyes; which again is homologous with the semi-medusiform,

fixed body of a Tubularia, and with the egg-producing process of the Hydra.

Now as all these bodies are homologous with one another, one of two conclusions is possible ; either, considering the Salpa mucronata to be an individual, we are logically led to look upon the egg-producing process of Hydra as an individual also, which seems absurd.

Or starting with the assumption that the egg-producing process of Hydra is a mere organ, we arrive at the conclusion that the Salpa mucronata is a mere organ also : which appears equally startling.

The whole question appears to turn upon the meaning of the word "individual."

This word the Lecturer endeavoured to show always means, merely, "a single thing of a given kind."

There are, however, several kinds of Individuality.

Firstly, there is what may be called *arbitrary* individuality, which depends wholly upon our way of regarding a thing, and is, therefore, merely temporary : such is the individuality of a landscape, or of a period of time ; a century for instance.

Secondly, there is an individuality which depends upon something else than our will or caprice ; this *something* is a fact or law of co-existence which cannot be materially altered without destroying the individuality in question.

Thus a Crystal is an individual thing in virtue of its form, hardness, transparency, and other co-existent qualities ; pound it into powder, destroy the co-existence of these qualities, and it loses its individuality.

Thirdly, there is a kind of individuality which is constituted and defined by a fact or law of succession. Phenomena which occur in a definite cycle are considered as one in consequence of the law which connects them.

As a simple instance we may take the individuality of the beat of a pendulum. An individual beat is the sum of the successive places of the bob of the pendulum as it passes from a state of rest to a state of rest again.

Such is the individuality of living, organized beings. Every organized being *has* been formless and will again be formless ; the individual animal or plant is the *sum* of the incessant changes, which succeed one another between these two periods of rest.

The individual animal is one beat of the pendulum of life, birth and death are the two points of rest, and the vital force is like the velocity of the pendulum, a constantly varying quantity between

these two zero points. The different forms which an animal may assume correspond with the successive places of the pendulum.

In man himself, the individual, zoologically speaking, is not a state of man at any particular moment as infant, child, youth, or man ; but the sum of all these, with the implied fact of their definite succession.

In this case, and in most of the higher animals, the forms or states of the individual are not naturally separated from one another : they pass into one another undistinguishably.

Among other animals, however, nature draws lines of demarcation between the different forms ; thus, among insects the individual takes three forms, the caterpillar, the chrysalis, and the butterfly. These do not pass into one another insensibly, but are separated by apparently sudden changes, each change being accompanied by a separation of the individual into two parts. One part is left behind and dies, it receives the name of a skin or cast ; the other part continues the existence of the individual under a new form.

The whole process is called Ecdysis : it is a case of what might be termed *concentric* fission.

The peculiarity of this mode of fission is : that of the two portions into which the individual becomes divided at each moult, one is unable to maintain an independent existence and therefore ceases to be of any importance ; while the other continues to carry on all the functions of animal life, and to represent in itself the whole individuality of the animal. From this circumstance there is not objection to any independent form being taken for, and spoken of as the whole individual, among the higher animals.

But among the lower animals the mode of representation of the individual is different and any independent form ceases, in many cases, to represent the whole individual ; these two modes, however, pass into one another insensibly.

The best illustration of this fact may be taken from the development of the Echinodenus, as it has been made known by the brilliant discoveries of Professor Müller.

The Echinus lividus stands in the same relation to its Pluteus as a butterfly to its caterpillar ; in the course of development only a slight ecdysis takes place, the skin of the Pluteus becoming for the most part converted into the skin of the Echinus.

But in Asterias the Bipinnaria which corresponds with the Pluteus gives up only a portion of its integument to the developed Asterias, the remaining and far larger portion lives for a time after its separation as an independent form.

The Bipinnaria and the Starfish are as much forms of the same individual as are the Pluteus and Echinus, or the caterpillar and butterfly; but here the development of one form is not necessarily followed by the destruction of the other, and the individual is, for a time at any rate, represented by two co-existing forms.

This temporary co-existence of two forms of the individual might become permanent if the Asterias, instead of carrying off the intestinal canal of the Bipinnaria, developed one of its own; and this is exactly what takes place in the Gyrodactylus, whose singular development has been described by Von Siebold.

But the case of the Gyrodactylus affords us an easy transition to that of the Trematoda, the Aphides, and the Salpæ, in which the mutual independence of the forms of the individual is carried to its greatest extent; so that even on anatomical grounds it is demonstrable that the difference between the so-called "skin" of the caterpillar, the free Bipinnaria, and the Salpa democratica is not in kind, but merely in degree.

Each represents a *form* of the individual; the amount of independent existence of which a form is capable cannot affect its homology as such.

The Lecturer then proceeded to point out that the doctrine of the "Alternation of Generations," and all theories connected with it, rest upon the tacit or avowed assumption "that whatever animal form has an independent existence is an individual animal," a doctrine which, he endeavoured to show, must, if carried out, inevitably lead to absurdities and contradictions, as indeed Dr. Carpenter has already pointed out.

There is no such thing as a true case of the "Alternation of Generations" in the animal kingdom; there is only an alternation of true generation with the totally distinct process of Gemmation or Fission.

It is indeed maintained that the latter processes are equivalent to the former; that the result of Gemmation as much constitutes an individual as the result of true Generation; but in that case the tentacles of a Hydra, the gemmiferous tube of a Salpa, nay, the legs of a Centipede or Lobster, must be called individuals.

And if it be said that the bud must have in addition the power of existing independently to constitute an individual, there is the case of the male Argonaut, which has been just shown by H. Müller to have the power of detaching one of its arms (a result of gemmation), which then leads a separate existence as the Hectocotylus.

Without a misuse of words, however, no one would call this a separate individual.

In conclusion the Lecturer stated his own views thus :

The individual animal is the sum of the phenomena presented by a single life : in other words, it is all those animal forms which proceed from a single egg taken together.

The individual is represented in very various modes in the Animal Kingdom : these modes pass insensibly one into the other in nature ; but for purposes of clear comprehension they may be thus distinguished and tabulated.

Representation of the Individual.

I. By Successive Inseparable Forms.

Ascaris. A. Forms little different = Growth.

Triton. B. Forms markedly different = Metamorphosis.

II. By Successive Separable Forms.

1. *Earlier Forms not Independent.*

Cockroach. A. Forms little different = Growth with Ecdysis.

Beetle. B. Forms markedly different = Growth with Metamorphosis.

2. *Earlier Forms partially Independent.*

Starfish.

III. By Successive and Co-existent Separable Forms.

a. External Gemmation.	*b. Internal Gemmation.*
A. Forms little different.	All the forms produce eggs.
Nais. *Hydra.*	*Gyrodactylus.*
B. Forms markedly different.	Last forms only produce eggs.

*** Last Forms produced.

Generally :

Medusa.	*Fluke.*

Locally :

Salpa.	*Aphis.*

These various modes of Representation of the Individual are ultimate facts. One is neither more nor less wonderful or explicable than another ; any theory which pretends to account for the Successive and Co-existent forms of the Aphis-individual must also

account for the Successive forms of the Beetle-individual or of the Horse-individual—since they are phenomena of essentially the same nature.

When the forms of the Individual are independent it becomes desirable to have some special name by which we may denote them so as to avoid the incessant ambiguity of the two senses of the word individual. For these forms the Lecturer some time ago proposed the name "Zöoid." Thus the Salpa-individual is represented by two Zöoids ; the Fluke by three ; the Aphis by nine or eleven, &c.

The use of this term is of course a mere matter of convenience and has nothing to do with the question of Individuality itself.

XVII

ON THE MORPHOLOGY OF THE CEPHALOUS MOLLUSCA, AS ILLUSTRATED BY THE ANATOMY OF CERTAIN HETEROPODA AND PTEROPODA COLLECTED DURING THE VOYAGE OF H.M.S. RATTLESNAKE IN 1846-50

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"THE mere description of appearances even of the interior structure, still less of the exterior surface of an animal, without the deductions which they legitimately yield, is of comparatively small value to the philosophic naturalist; for of what value are facts until they have been made subservient to establishing general conclusions and laws of correlation, by which the judgment may be safely guided in regard to future glimpses at new phenomena in nature?'[1]

If I prefix this admirable exposition of the true aims of anatomical investigation to the present essay, it is that I may justify, by the highest authority, the course which I have taken in considering what of new facts it contains, as of subordinate importance to the reasonings which may be based upon those facts; in making its scope more morphological than zoological.

The morphology of the Cephalous Mollusca is a subject which has been greatly neglected. No Savigny has determined the homologies of their different organs, and so furnished the only scientific basis for anatomical and zoological nomenclature.

It is not settled whether the back of a cuttle-fish answers to the dorsal or to the ventral surface of a Gasteropod. It is not decided whether the arms and funnel of the one have or have not their homologues in the other. The dorsal integument of a *Doris* and the cloak of a Whelk are both called "mantle," without any evidence to show that they are really homologous.

Nor do very much more definite notions seem to have prevailed

[1] Owen, Anatomy of *Spirula*, Voyage of Samarang, Zoology, p. 12.

with regard to the archetypal molluscous form, and the mode in which (if such an archetype exist) it becomes modified in the different secondary types. So far as our knowledge goes among other forms of animal life, we invariably find that, whatever the subsequent variations and aberrations, the primordial embryonic form has its parts arranged symmetrically about a given axis.

No one imagines the Pleuronectidæ belong to an asymmetrical type because they are asymmetrical in their adult shape, and yet there is no stronger evidence for the very common assertion that the typical form of the Mollusca is spiral or asymmetrical.[1]

This unsatisfactory state of our knowledge appears to me to result from two causes ;—first, from the want of a clear and definite conception of the fundamental varieties of molluscous structure, and of the nature of the changes in the relations of parts which constitute those varieties ; and secondly, from the want of a due regard to the facts presented by the development of the different families, which must stand in the relation of cause to the varieties of form.

Now in order to the former end (the obtaining of a definite conception of the varieties of molluscous form), I propose to set forth the structure of certain Heteropoda and Pteropoda ; pelagic animals so transparent, that a perfect knowledge of the arrangement of their parts may be arrived at by simple inspection, without so much as interrupting a beat of their heart.

Afterwards I shall inquire how far the known laws of development account for these forms, and thence of what archetypal form they may be supposed to be modifications.

PART I.

I. *Anatomy of Firoloïdes* (Plate II. [Plate 17] fig. 1).

The species of *Firola* which I examined appears to be identical with the *Firoloïdes Desmarestii* of MM. Eydoux and Souleyet.[2]

The animal may be described as a transparent cylinder about an inch long, and so generally colourless as to be hardly distinguishable in the water, except by the incessant flapping of its flattened ventral appendage (*pp*).

The only parts which present any colour are the buccal mass, which is brownish ; the eyes, almost black, and the mass of the liver, which is brownish-green ; further, the anus has a pinkish tint.

[1] See Von Baer, Nova Acta Acad. Nat. Cur. vol. xviii. p. 753.

[2] Figured by them in their beautiful plates illustrative of the Zoology of the Voyage of the Bonite.

Attached by a narrow root or pedicle to the ventral surface of the cylindrical body is the broad cheese-cutter-shaped foot, or as I propose to call it, *propodium* (*pp*). Its posterior edge is quite sharp, and carries no sucker-like expansion. The anterior fifth, or thereabouts, of the animal is thinner than the rest of the body, and it narrows again towards its extremity, which is truncated, and forms a circular lip round the aperture of the mouth. Just behind the narrowed fifth, and towards the dorsal surface, we observe the eyes, and immediately below, and as if proceeding from them, are the tentacles, which are short and conical.

The posterior extremity also is abruptly truncated ; its uppermost angle slightly projects, and viewed from above appears like a subspiral, richly ciliated band (*d*). Some little distance from this is the aperture of the anus (*a*).

From the two inferior angles, two tubular processes pass in the male (fig. 1). The right process ends in a globular body and is the penis (*p*), while the left (which I shall call the *metapodium*) is long and somewhat pointed (*mt*).

In the female there is only one process (the metapodium) (figs. 2, 3 *mt*) answering to the left of the male, but a long cylindrical egg-tube frequently trails from the aperture of the oviduct (fig. 2).

Alimentary System.—This consists of,—1, the buccal mass ; 2, the œsophagus and stomach ; 3, the intestine and its termination, the rectum ; 4, the liver ; and 5, the salivary glands, which are very small and placed above the buccal mass, contrasting singularly with the very large salivary glands of *Atlanta.*

The œsophagus, stomach, and intestine form a straight tube running through the axis of the animal, and suspended by a ligament to the dorsal parietes (fig. 1) ; having reached the " nucleus," that is, the mass of the liver and ovary, the intestine bends up at a right angle, and so becomes the rectum, which terminates, as has been seen, upon the dorsal surface.

The Buccal Mass, or Tongue (fig. 1 *b*).—This is an oval brownish body, placed below the commencement of the œsophagus, and forming the floor of the cavity of the mouth. The following parts may be distinguished in this mass :—

1. Two ovoid compressed masses of thick-walled clear cells, which somewhat resemble cartilage. I shall call these the " lingual cartilages."

2. These give attachment to muscular fibres by their outer surface, and are enveloped in them. One portion of these fibres is inserted anteriorly into the parietes of the body, and acts, therefore, as a

protractor. The rest are inserted into the edges of a thin plate, the "tongue-plate," which is closely applied to the whole of the upper and a part of the anterior lower surface of the cartilages, being as it were bent over their anterior extremities. The applied surfaces of the plate and of the cartilages are perfectly smooth, so that the former can play readily over the latter, like a rope upon its pulley. The upper surface of the tongue-plate carries in the middle a single row of tridentate teeth; outside these is a row of conical spines and broad flat-edged plates, and most externally there are one or more rows of recurved hooks, which, when the organ is at rest, lie over and nearly meet one another in the middle line.

When this organ is in action, it is commonly more or less protruded from the mouth by the protractor muscles; the large lateral spines of the tongue are divaricated (giving rise to that resemblance to the oral armature of *Sagitta* which has been remarked), so as to get all the teeth to bear; and then by the alternate action of the upper and lower sets of muscles inserted into the tongue-plate, a chain saw-like movement is communicated thereto, in consequence of which the teeth act as a rasp or saw upon any body with which they are brought in contact.

The buccal cartilages take no part in the movement of the tongue-plate, but simply act as its pulley.

The *Œsophagus* widens so gradually into the stomach, that no distinct line of demarcation can be drawn between the two, but the latter narrows suddenly into the intestine at a short distance in front of the "nucleus."

The *Liver* (*l*) is composed of several foliaceous masses containing many oil-globules; it opens by a wide duct into the angle of junction of the intestine and rectum.

The Circulatory System (figs. 1, 2, 3, 6).—This consists of a very perfect heart with an aorta and its branches, but there is no trace of any venous system.

The heart lies anterior to and parallel with the rectum; its axis, therefore, is nearly at right angles with that of the body. It possesses two chambers, an auricle (*u*) and a ventricle (*v*). The auricle is large and somewhat elongated, extending above into the elevation which carries the subspiral ciliated band. Its wall is formed by branched and interlacing muscular fibres, which are attached partly to the parietes, partly to the walls of a contractile sac (*c*), to be mentioned presently.

The ventricle is almost globular, and has thicker walls, in which the separate muscular fibres are not distinguishable. The lips of the

auriculo-ventricular aperture are prolonged on the ventricular side into two valvular folds. Below, the ventricle terminates in a wide aorta, which immediately gives off a large branch backwards to the hepatic and generative organs; then becoming much convoluted, it runs forwards along the intestine and stomach, passing between the latter and the pedal ganglia (fig. 6), and finally terminating, without much alteration in its diameter, in the buccal mass.

As it passes over the pedal ganglia it gives off a considerable branch, "the pedal artery," downwards to the foot; and this pedal artery, just before it enters the foot, gives off a long and delicate "metapodal" branch (w'), which passes backwards, parallel to the aorta, and finally terminates in the metapodium, figs. 2 and 3.

The mode of ending of the pedal artery is very remarkable, and physiologically speaking, almost unique (fig. 6). Having entered the foot, it ends suddenly, without narrowing, in a truncated open extremity (y'). In the living animal this open end possesses the power of contracting to a very great extent, so as almost to become closed; and its condition must necessarily exercise a very considerable influence upon the direction and rapidity of the animal's circulation.

Firoloïdes[1] then affords the most complete ocular demonstration of the truth of M. Milne-Edwards's views with regard to the nature of the circulation in the Mollusca, that can possibly be desired. The perfect transparency of the creature allows the corpuscles of its blood to be seen floating in the visceral cavity between the intestine and the parietes, and drifting more or less rapidly backwards to the heart. Having reached the wall of the auricle, they make their way through its meshes as they best may, sometimes getting entangled therein, if the force of the heart has become feeble. From the auricle they may be followed to the ventricle, and from the ventricle into the aorta, whence they pass, some forwards, to the buccal mass, in which the aorta ends, and through whose tissues it pours them; some downwards, to pour out of the widely open end of the pedal artery, flooding the tissues of the propodium; and a small proportion passes directly backwards to the visceral mass and to the metapodium.

Respiratory System.—So delicate a creature would hardly seem to need any special system of this kind, and I found no trace of such organs in any, even the freshest and most uninjured specimens.

In the nearly allied species *Firola Keraudrenii*, however, the gills appear as a row of conical processes, extending along the posterior

[1] A similar condition of the circulatory system has been observed by Nordmann, Quatrefages, Van Beneden, and Allmann, in various Nudibranchiata, though perhaps not quite so distinctly.

edge of the body behind the anus ; and in other species such processes develope accessory folds, until in *Carinaria* we find fully-formed branchiæ (see Eydoux and Souleyet). The ciliated subspiral band (*d*) which will be found to have its homologue in *Atlanta*, is the only structure which appears to be capable of assisting the respiratory function ; but its small size must render it of very little importance.

Mantle.—There is no distinct mantle in *Firoloïdes Desmarestii.*

Carinaroides (Eydoux and Souleyet) evidently forms the transition from the Heteropods without a mantle to those with one. It is in this genus placed at the lower posterior angle of the body, and carries a minute shell ; the branchiæ are developed between it and the anus.

In *Carinaria* there is a proportionably small mantle and shell, but it occupies a position more resembling that of ordinary Mollusks ; and in *Atlanta*, as will be seen, the relative proportions of the mantle and body are pretty nearly those found in ordinary Gasteropods.

Contractile Sac or Urinary Organ (*c*, figs. 2, 3).—Between the rectum and the heart, and therefore bathed by the returning venous blood, there lies an elongated, flattened, delicate, and transparent sac, whose walls are usually very much wrinkled and sacculated.

This sac opens by a rounded aperture in its upper part upon the right side of the animal, and is, of course, continually filled by the surrounding water. As the sac is incessantly contracting, however, this water must be continually renewed, and hence the organ, simple as its structure appears and small as its size may be, is probably a very efficient depurating agent.[1]

Considerations to be stated hereafter, lead me to the belief that it is in fact the urinary organ, at once kidney and urinary bladder.

Reproductive System.—*Firoloïdes* is diœcious. The male may be distinguished at once from the female, by the peculiar penis (*p*) attached to the right posterior inferior angle of the body (fig. 4). It consists of two portions ; the larger is cylindrical, but enlarged at its extremity into a globular head, from one side of which a small pointed process projects. The globular body contains many large cells as a sort of lining, and within these there is a cavity which communicates with the exterior through the pointed process. A vast number of small oval fatty-looking particles may be made by pressure to pass out from the cavity.

The smaller portion is like a trifid leaf ; it is placed at the base

[1] In the "Explication des Planches," Eydoux and Souleyet call a similar organ in *Firola* "organe de la dépuration urinaire ?".

of the former portion, and almost reminds one of the sculptor's vine-leaf.

The *Testis* is not very easily to be distinguished from the liver, behind which it is placed, until the contained spermatozoa are recognized. It occupies about the posterior half of the nucleus. There is hardly any proper vas deferens, but the testis opens by a very short canal at the base of the penis.

The *Ovarium* (*o*) occupies a position similar to that of the testis (figs. 2 and 3). A wide oviduct arises from it about its centre, on the right side, and after making one bend, passes downwards, and opens close to the base of the metapodium.

The ovarian ova were oval, about $\frac{1}{300}$dth of an inch in diameter, with a clear, delicate, germinal vesicle about $\frac{1}{600}$dth of an inch in diameter, and a pale, circular, clear, but thick-walled vesicular germinal spot about $\frac{1}{1000}$dth of an inch in diameter. In the oviduct the ova possessed either an entire granular yelk, in which I could not detect any germinal vesicle, or the yelk was broken up into two or more (but not many) spherical or subspherical masses, containing a clear vesicle, the embryo-cell.

In some individuals a long tube (figs. 2 and 5), half as long as the body or more, depended from the orifice of the oviduct. It was colourless and transparent, and appeared as if articulated from its membrane being thrown into regular annular folds.

This egg-tube contained a double series of ova, in which the yelks had undergone division into 8 to 15 masses of very variable size. The ova seemed to have become more divided the nearer they were to the distal extremity of the tube, but I could find none containing a distinct embryo.

The Nervous System (figs. 6 and 7).—Two three-lobed ganglia, closely applied together by their inner edges (fig. 7), are placed between the eyes. Each gives off several branches to the parietes and the following important trunks:—

1. A long branch forwards, which terminates in a small ganglion (β) placed in the angle of union of the œsophagus with the buccal mass, and joined to its fellow by a very short commissure beneath the œsophagus. From these "buccal ganglia" various small nerves are given off forwards to the buccal mass and parts about the mouth, and backwards, to the œsophagus.

[1] According to Milne-Edwards (Sur divers Mollusques, Annales des Sciences, 1842), a perfectly similar penis is found in *Carinaria*. He states, however, that the vas deferens traverses one portion of this organ, which is certainly not the case in either *Firoloïdes* or *Atlanta*.

2. A large optic nerve (*i*).

3. A nerve to the tentacle.

4. A small nerve from the under surface, which terminates in the auditory sac (*j*).

5. A large and long commissural branch which runs backwards and downwards past the stomach, to unite with the pedal ganglion of its side.

The *Pedal Ganglia* (*y*) are two large ovoid masses in contact by their inner edges. They give off—

1. Two branches downwards to the propodium.

2. Two branches upwards to the dorsal parietes.

3. Two large branches, which run at first separately below the stomach, and then unite to form a single trunk. This runs along the stomach and intestine, sometimes twisting round them and giving off branches to them and to the parietes; and on the intestine it separates again into two chords, which join two small ganglia (3) placed between the aorta and the intestine; one lies on the aorta, the other between this vessel and the intestine, and they are connected by a commissure. From the former of these ganglia, which is the smaller, two nerves pass upwards and join a flattish mass placed immediately beneath the "subspiral ciliated band." There was an obscure appearance of branches radiating from this mass, and it is probably ganglionic.

Organs of Sense. The Eyes (fig. 8).—The eyes are very perfectly organized; each eye is contained within a chamber, excavated in a papilla, whose convex wall forms a sort of supplementary cornea, answering to the cornea of Cephalopoda, or to the corresponding cutaneous cornea of the Gasteropoda.

Their eye-proper is suspended within this chamber by a number of irregular muscular bands, which stretch from it to the walls of the chamber, and perform the function of *oculi-motores*. The optic nerve penetrates the inner wall of the chamber and enters the eye from that side.

The eye-proper is elongated and somewhat hour-glass-shaped, being contracted just behind the crystalline lens. The constriction divides the eye into two portions, an internal and an external. The latter is almost spherical, and is formed by the true cornea, which is much thicker in the middle than elsewhere, so as to present a meniscus section. Behind, the cornea is continuous with the sclerotic coat, which is thick, and seems to be continuous with the neurilemma of the optic nerve.

The crystalline lens is spherical, and is separated by a very small

interval from the cornea, so that there is hardly any anterior chamber of the eye. There is no iris, but the inner surface of the posterior chamber is coated by a layer of dark chocolate-coloured pigment.[1]

The Auditory Vesicles (*j*), fig. 7.—These lie behind and a little below the cephalic ganglia. Each is a spherical vesicle, about $\frac{1}{300}$dth of an inch in diameter. Its walls are irregularly thickened here and there, and it contains a spherical otolithe of about half its diameter. I was unable to perceive any motion in the otolithe. The auditory nerve is a delicate thread arising from the under surface of the supra-œsophageal ganglion, just in front of the commissural cord. It appears to terminate suddenly on entering the vesicle.

This origin of the auditory nerves from the cephalic ganglia, *when the pedal ganglia are well marked and placed below the œsophagus*, is a circumstance common to all the Heteropoda,[2] and, so far as I am aware, altogether peculiar to them among the Mollusca. The only writers who appear to have been struck by it are MM. Frey and Leuckart: they say that the auditory organs are united with the supra-œsophageal ganglia "only when the lower œsophageal ganglia are wanting (except in *Carinaria*, in which the great length of the lateral commissures of the œsophageal ring appears to have made such a position necessary)." (Beiträge, p. 55.) I must confess I do not see the force of this explanation; and the lower œsophageal ganglia are never "wanting," though they may be united with the upper ones.

II. *Anatomy of Atlanta.* (Plate III. [Plate 18])

This is a very small and very beautiful pelagic mollusk, with a shell not more than one-fourth of an inch in diameter. It appears to be identical with the *Atlanta Lesuerii* of Eydoux and Souleyet. Its structure resembles that of *Firoloïdes* in all its essential points, and the transition between the latter and *Atlanta* is complete through such forms as *Firola*, *Carinaroides*, and *Carinaria*.

The shell is flattened and spiral, none of the whorls projecting beyond the plane of the outermost. The aperture is notched on its

[1] I do not see that the eyes of Heteropoda are so "peculiarly formed" as Krohn has it (Ferner Beiträg zur Kenntniss des Schneckenauges. Müller's Archiv, 1839). What I have described as the true cornea, is by Krohn considered as an anterior portion of the vitreous humour; such an arrangement would of course be very peculiar, but I think that my account is correct. The eye, it would appear, projects much less in *Carinaria* and *Pterotrachea*; and in the latter, according to Krohn, there is even a rudimentary eyelid.

Krohn does not say anything about the muscles of the eye in these two genera.

[2] Compare Milne-Edwards, Sur divers Mollusques, Annales des Sciences, 1842, and the figures of Eydoux and Souleyet, so often referred to.

dorsal edge, and a deep thin crest surmounts the outer whorl, and is generally broken in several places. The surface of the shell is marked by delicate transverse striations.

The outer fourth of the outer whorl of the shell is occupied by the mantle, the rest of the spire containing the viscera.

When protruded, the body of the animal is as large as the shell and appears trifid ; the large head forming the anterior division, the "fin" the middle, and the "tail," with its operculum, the posterior division.

The head is large and subcylindrical. Its anterior extremity is formed by a circular lip surrounding the mouth. The eyes are placed far back, and the longish conical tentacles proceed from the anterior part of their base.

The fin or "propodium" (*pp*) is flattened and fan-shaped ; its edge is provided with many long and delicate hairs, and its surface is covered with little asperities. Just below its point of attachment, the posterior edge of the propodium carries a cup-shaped disc (*ms*), also fringed with long hairs. This is commonly called the "sucker," and has no representative in *Firoloïdes*. It may be called the *mesopodium*.

The "tail" or *metapodium*[1] (*mt*) is subcylindrical at its base, but becomes flattened and acuminated inferiorly. The elongated lanceolate transparent operculum is fixed upon its posterior surface.

The animal moves by the vigorous flapping of its fin. When it withdraws within its shell the head is just retracted, then the fin is folded in, and finally, the tail with its operculum covers up the whole.

The male is distinguished from the female by the presence of a peculiar leaf-like penis (*p*), which is attached upon the right side of the body just above where it divides into the three portions of the foot, fig. 1.

The *Alimentary Canal* commences above an oval buccal mass, widens gradually into the stomach, then narrows again and opens into a quadrangular sac, which communicates with the liver. From the anterior and upper part of this sac the rectum is continued and runs forward to the upper and dorsal part of the branchial cavity, in which it terminates by a tubular anus.

The mechanism of the tongue exactly resembles that of *Firoloïdes*. Two long cylindrical salivary glands (*f*) open into the anterior part of the œsophagus. They are simple cæca lined by a thick epithelium.

The *Liver* (*l*, fig. 3) is a wide conical sac with sacculated and

[1] That this is the same organ as the metapodium of *Firoloïdes*, will be obvious upon comparing the different forms which it assumes in *Carinaria*, *Carinaroïdes*, and *Firola*.

glandular walls ; its communication with the quadrangular dilatation of the intestine is so wide that it may almost be considered as a diverticulum thereof, and it extends back as far into the spire of the shell as any of the viscera.

The rectum is of a pinkish colour, and is richly ciliated internally.

Circulatory System (figs. 2, 3, 4).—The heart resembles that of *Firoloïdes*, and consists of an auricle (*u*) and a ventricle (*v*). It lies parallel to the rectum, with the auricle forwards at the base of the mantle-cavity, and the animal is therefore prosobranchiate. The aorta proceeds from the apex of the ventricle, and immediately after its origin divides into two branches, one of which runs backwards to the visceral mass, while the other passes forwards close beneath the stomach, until it terminates in the buccal mass. After passing over the subœsophageal ganglia, it gives off a downward branch to the fin, but I did not observe the peculiar termination of this artery which obtains in *Firoloïdes* ; this perhaps may be accounted for by the greater muscularity of the fin in *Atlanta*, rendering it less transparent. The venous blood has no distinct channel, but returns to the heart by the cavity of the body. The returning current of blood-corpuscles is very obvious ; they seem to pass quite freely in all directions round the intestine, aorta, and nervous centres, the general tendency being always backwards towards the heart.

Respiratory System.—Very distinct gills are figured by Eydoux and Souleyet in most Atlantæ, but their presence in this species was decidedly exceptional, the majority of specimens presenting no trace of them. Once I noticed a bundle of long branchial filaments depending from the wall of the mantle-chamber ; and in another case rudimentary and undeveloped short processes of the same kind were to be seen ; they contained canals, through which a small portion of the returning venous blood was diverted, fig. 4.

The *Mantle* is very well developed ; a peculiar thickened and ciliated band crosses it transversely, and seems to be the homologue of the subspiral ciliated band in *Firoloïdes* (*d*).

Contractile Sac.—This resembles the corresponding organ in *Firoloïdes* ; it lies between the rectum and the heart, and opens into the bottom of the chamber of the mantle by a well-defined oval aperture, figs. 3 and 4 *c*.

Generative Organs.—The ovary or testis is an elongated mass corresponding to the liver, and occupying the inner and right half of the visceral mass, fig. 3 *t*.

The *Ovary* consists entirely of a mass of ova in course of development, with their characteristic germinal vesicle and spot. The oviduct

commences at its anterior larger extremity ; it is very wide and passes forwards, forming many convolutions, and terminates in the mantle-cavity by the side of the anus.

The *Testis* contains a mass of small cells and spermatozoa in various stages of development. The vas deferens leads from its anterior extremity, and before terminating in the cavity of the mantle, dilates, occasionally forming thus a dark spherical vesicula seminalis, *s*, fig. 3.

There is a kind of penis attached to the right side of the neck of the animal just above the foot (*p*, fig. 1): it is composed of two portions arising from a common base. The anterior and inner is like a three-pointed leaf ; a cæcal ciliated canal runs along its centre. The posterior portion is a tubular cylindrical process, with a kind of ciliated cup at its extremity (fig. 5): a conical body projects into this below. The tube is nearly filled with small oval granules. The resemblance between this and the penis, which has been described in *Firoloïdes*, cannot be misunderstood, and the position of the organ in *Atlanta* corresponds with that in *Firoloïdes*, if we consider the left filamentous process in the latter to be the metapodium. That it is so, is demonstrated not only by the distribution of the metapodal arteries, but by an examination of the intermediate genera above mentioned.

Nervous System (figs. 2 and 6).—This consists of two trilobed supraœsophageal ganglia (fig. 6), which correspond to those of *Firoloïdes*, and give off similar nerves ; but in addition their posterior lobes give off each a long nerve,[1] which runs back upon the stomach, and below its posterior narrowing, between this and the aorta, joins with its fellow in a small ganglion (not figured by Eydoux and Souleyet) ; some branches pass from this to the viscera, and two or three run in the substance of the mantle to the " ciliated band," fig. 4.

The commissural cords which unite the supraœsophageal with the subœsophageal or pedal ganglia, are at first double (fig. 6), but afterwards unite into one. They are connected with the subœsophageal or pedal ganglia (*y*), two large oval masses from which several branches are given to the different parts of the foot ; and each gives off one long cord which runs along the lower surface of the intestine, and probably joins the ganglion upon the aorta before mentioned.

The *Eyes* (*i*, fig. 6) resemble those of *Firoloïdes*, except that their pigment is black.

The *Auditory Vesicles* are spherical and about $\frac{1}{380}$th of an inch in

[1] In *Carinaria* a similar commissural nerve, between the cephalic and the parieto-splanchnic system of ganglia, has been shown to exist by Milne-Edwards (*loc. cit.*), but I could find none in *Firoloïdes*.

diameter. Each contains a single strongly refracting globular otolithe of about $\frac{1}{800}$dth of an inch in diameter. In some cases this had a slow movement of rotation upon its axis, fig. 6, *j*.

Now in regarding *Firoloïdes* and *Atlanta*, whose structure has just been described, as illustrations of a typical form, the following circumstances appear to me to be of importance :—

1. The intestine is bent dorsal, or towards the side on which the heart is placed. The visceral mass is situated below and behind the posterior portion of the alimentary canal ; it may be called a post-abdomen.

2. *Atlanta* is prosobranchiate ; *Firoloïdes* is neither opisthobranchiate nor prosobranchiate.

3. The foot consists of three parts, the propodium, mesopodium, and metapodium, in *Atlanta* ; but of these the mesopodium disappears in *Firoloïdes*, and the metapodium becomes very rudimentary.

4. The auditory organs appear to be connected with the cephalic ganglia.

5. The animals are unisexual.

III. *Anatomy of Pteropoda.* (Plate IV. [Plate 19])

The variation of form undergone by the members of this group is perhaps greater than that which takes place in any other, except it may be the Nudibranchiata, and hence their structure is particularly instructive.

Three very distinct modifications of the type present themselves at first sight. The first is characterized by the non-development of the mantle and the full development of the foot, ex. *Pneumodermon*, *Clio*, fig. 1.

The second, by the great development of the mantle, by its cavity opening upon the ventral surface, and by the minuteness or absence of the mesial portion of the foot, ex. *Cleodora*, fig. 4.

The third resembles the second, but the mantle-cavity is placed upon, or at any rate opens upon, the dorsal surface, ex. *Spirialis*, *Limacina*.

1. It is very remarkable that Cuvier should not have recognized in the " espèce de menton," and the " deux petits lèvres "[1] of *Pneumodermon*, nor in the " deux tentacules triangulaires " of *Clio*,[2] the homologues of the foot of the Gasteropoda. In fact, it was on the strength of their having no such appendage that he founded his new order of

[1] Mém. sur le Pneumoderme, p. 7.

[2] Mém. sur le Clio, p. 6.

Pteropoda,[1] and yet the resemblance of the inter-alar appendages in these two genera [2] to the foot of Gasteropods is so striking as at once to point to their real nature.

In truth, the foot, though very small in these genera, is exceedingly well-marked, and shows a clear division into mesopodium and metapodium. It may be a matter of doubt whether the propodium is developed or not, and this question can be settled by embryology alone; but for the present, I think, it may be fairly presumed that it is represented by the tentaculigerous hood of *Pneumodermon* and by the tentaculigerous lobes of *Clio*; following in this case a very common tendency (exemplified in all the Cephalopods and in many Gasteropods) to become developed over and in front of the mouth.[3]

As Cuvier demonstrated, there is no "mantle" in *Pneumodermon* and *Clio*;[4] the body of these mollusks answering precisely to that of a *Firoloïdes*. The relation of the gill-laminæ and of the small anomalous shell in *Pneumodermon* sufficiently corroborates Cuvier's view. Gills are never placed upon the outer surface of a mantle; and if anything answers to such an organ it must be the small space covered by the rudimentary shell, so that the relations of the parts are, in fact, similar in *Pneumodermon* to what we find in *Firola* and *Carinaroides*.

Finally, new parts, the "alæ," make their appearance in these genera and give its character to the order (figs. 1, 2, 3, 4, 7, *ep*).

Considering the position and relation of these organs as distinct developments from the upper part of the sides of the foot, and the fact that their nerves arise, like those of the foot, from the pedal ganglia, I propose to consider them as parts of the foot and to call them the "epipodia." It has been long since shown by Van Beneden and others that they have nothing to do with the respiratory function.

In this subtype the intestine opens on the right ventral side of the neck, and dissection shows its first bend to be ventral, that is, towards the side of the pedal ganglia.

[1] Mém. sur le Clio, p. 9; sur l'Hyale et le Pneumoderme, p. 10.

[2] This is fully recognized by Leuckart, "Ueber die Morphologie," &c. p. 149.

[3] The origin of the nerves of the acetabuliferous tentacula may probably throw some light upon this matter; I have not had the opportunity of dissecting sufficiently large specimens of either *Pneumodermon* or *Clio*, carefully, with regard to this especial point. From the figures of Eydoux and Souleyet, one would be led to believe that the nerves of the acetabuliferous tentacles arise from the cephalic ganglia, which would be a very great objection to the view advocated above, since all the other parts of the foot, the mesopodium, metapodium, and epipodium are supplied by the pedal ganglia. (See Eydoux and Souleyet, plate 15, fig. 30, and plate 15 bis, fig. 8.)

[4] Eydoux and Souleyet, however, call it "manteau" in the description of their figures. Leuckart also opposes Cuvier's view, but I think without reason. (*Op. cit.* p. 146, note.)

2. The genus *Psyche*[1] or *Euribia* offers a very interesting transition from the foregoing to the second subtype. This genus is commonly said to have a cartilaginous shell, but this so-called shell appears, upon careful examination, to be only the thickened integument of the body; it is not secreted by a true mantle, like that of *Cleodora*, &c. The notion of a shell has arisen seemingly from the fact that a sort of cleft exists anteriorly from which the locomotive organs of the animal can be protruded and into which they can be retracted, but at the margin of this cleft the softer parts of the body are continuous with the harder, just as the body of a Polyzoon is connected with its cell.

In some individuals I have observed the posterior extremity of the body to be surrounded by two circlets of cilia.[2]

The head of the animal is provided with two very large tentacles,[3] which carry a large process upon the inner side of their base, and rudiments of eyes upon the outer. Between the tentacles on the ventral side are two projecting lips with the aperture of the mouth between them, fig. 3.

Behind the mouth there are two lobes, separated by a deep notch; these are the two portions of the mesopodium which had begun to be separated in *Clio*. Behind these, again, there is a single tongue-shaped lobe, the metapodium, which is continuous on each side with two elongated and expanded epipodia.

There are no gills, and the anus opens ventrally upon the left side.

From this genus, to that called *Criseis* by Rang, but which Eydoux and Souleyet unite with *Cleodora*, the transition is very easy, figs. 6, 7.

In these forms there is an elongated conical shell, narrow and straight, or wider and slightly curved at its extremity. The body puts one in mind of that of a Cephalopod, being enveloped in a wide mantle, which is united to the body on the dorsal side only (fig. 6). The wall of the mantle is very thick, so that it presents a wide aperture always open upon the ventral side. Its free edge is, as it were, cut down upon its dorsal side, so that ventrally it is considerably longer. On the right side this prolonged portion has a rectangular edge, but upon the left it forms a sort of ram's-horn process.[4] The lower part of the inner surface of the mantle is richly ciliated, and

[1] My species appears to be the *Euribia Gaudichaudii* of Eydoux and Souleyet.

[2] It is a very interesting fact that Professor Müller has found the larvæ of *Pneumodermon* to be provided with similar ciliated bands, Ueber die Entwickelungs-formen, &c. Monatsbericht d. k. Akad. d. Wiss. zu Berlin, October, 1852.

[3] These are called "branchies" by Eydoux and Souleyet (pl. 15), but why I cannot divine, since these organs are certainly homologous with the tentacles of *Cleodora*.

[4] Is this to be compared with the small posterior curved process of the edge of the mantle in Gasteropteron?

is raised into a number of transverse ridges, which must probably be considered to be rudimentary gills.

The head and wings are united with the part of the body covered by the mantle, by a narrow neck ; compared with *Euribia*, the change in form is such as would be produced by a lateral expansion of the foot. Behind the mouth is the wide metapodium, and on each side of it are the broad epipodia continuous with the metapodium. About midway between the mouth and their margin the epipodia carry a small triangular lobe (*ms*), which evidently represents one-half of the mesopodium ; and nearly at the same level, on their anterior edges, they present two small curved and pointed processes, the representatives of the large tentacles of *Euribia*. Two minute papillæ, the rudiments of the eyes, are placed upon the dorsal surface just behind the anterior edge of the alæ (*i*).

The œsophagus takes a straight course backwards from the mouth, which contains a minute lingual prominence, and widens gradually into a pyriform muscular gizzard, which is provided with two strong curved and conical teeth. The intestine passes from the narrow pylorus, and preserving the same width throughout, bends downwards towards the ventral side, and ultimately terminates in the cavity of the mantle a little to the left of the mesial line, fig. 6.

Just behind the pylorus a very long straight cæcum is given off and sometimes there is a short one in addition by the side of it. The parietes of these sacs are glandular.

A long "columellar" muscle attaches the animal near to the apex of its shell, and then passes down into the foot, where it spreads out.

The position of the heart varies remarkably in this genus, and this variation is still more remarkable, if, with Eydoux and Souleyet, we consider it to be one with *Cleodora*.

In *C. aciculata* (figs. 6, 7) the mantle-cavity extends considerably beyond the transversely-barred portion of the mantle, and the base of the auricle abuts upon its lower posterior portion. The apex of the heart points backwards and a little to the left side, and in M. Milne-Edwards's arrangement the animal would be prosobranchiate. In *C. virgulata* (E. and S.) the base of the auricle lies behind the right posterior portion of the mantle-cavity, and the apex of the ventricle points directly to the left ; it is therefore neither prosobranchiate nor opisthobranchiate.

In *Cleodora curvata*, on the other hand, as will be seen immediately, the base of the auricle is posterior and the ventricle points forwards ; it is opisthobranchiate, figs. 4 and 5.

In this one genus, then, we have every transition from the prosobranchiate to the opisthobranchiate type of organisation.

The aorta is too delicate to be readily traced in *C. virgulata* and *C. aciculata*. It may, however, be seen passing through the nervous ring and bifurcating for the epipodia, fig. 7 *w*. There is no rudiment even of a venous system.

The *Cleodora curvata* (figs. 4 and 5) (one of the true *Cleodoræ* as formerly defined) forms a transition from the preceding species to *Hyalæa*. It has the general organization of the former, with the flattened shell more or less fissured laterally, and the filiform appendages to the mantle, of the latter.

The alary expansion forms a more rounded disc than in *C. aciculata* and *virgulata*, the metapodium having become widened out and almost undistinguishable from the epipodia. The triangular lobes, rudiments of the mesopodium, have disappeared.

The intestinal canal resembles that of the two former species ; its flexure is ventral, and the anus opens into the cavity of the mantle on that side. The long cæcum has orange-coloured glandular parietes.

The position of the heart has been described. It is comparatively large, and the aorta may be readily traced from it, passing forwards over the stomach and through the nervous ring, and eventually dividing into two branches, one for each epipodium.

There is a more distinct rudiment of a venous system in this mollusk than in *Firoloïdes* or *Atlanta*. A wide canal traverses the mantle towards its upper part ; it is crossed by various muscular bands. Another distinct canal can be traced from the auricle towards the right side, skirting the lower border of the branchial chamber. Whether it becomes continuous with the right extremity of the previous canal or not, I could not certainly determine. The blood flows from both ends of the first-mentioned canal towards the auricle, but on the left side there does not appear to be so distinct a venous canal as on the right.

In all species of *Cleodora* there is an elongated sac, in its structure, contractions, and position relatively to the heart, exactly resembling that of the Heteropoda. It communicates by a small aperture with the cavity of the mantle.

The *nervous system* in all these species consists of three ganglia on each side of the œsophagus. Four of these form a mass, placed entirely below the œsophagus, and the other two, placed in contact with and immediately above them at the side of the œsophagus, are united above by a broad flattened supraœsophageal commissure.

The upper (*cephalic*) ganglia give off two principal branches to the

rudimentary eyes and tentacles. The anterior pair of the lower mass (the *pedal* ganglia) give off branches to the epipodia and expansion of the foot generally ; posteriorly they carry two small auditory vesicles, with many otolithes.

The posterior (*parieto-splanchnic*[1]) ganglia give off their principal branches to the mantle.

The aorta passes between the pedal and parieto-splanchnic ganglia.

3. I have mentioned that a third subtype appears to be formed by *Spirialis* and *Limacina*, which are the only Pteropods with spiral shells. *Spirialis*, again, is the only Pteropod with an operculum. But a more important difference for my present purpose consists in the fact that in these genera the mantle-cavity (and with it the anus) opens on the dorsal side of the animal. I have not myself been fortunate enough to obtain specimens of these genera, and as the attention of those anatomists who have examined them does not appear to have been specially directed to this point, it is impossible to make out with certainty whether the first flexure of the intestine is also dorsal, or whether, as in all other Pteropods, it is ventral. I cannot think that any real variation will be found to occur among closely allied forms, in a matter so fundamentally connected with their whole structure and mode of development ; and I would suggest that here also the bend of the intestine is truly ventral, but that by a continuation of the process by which the anus is thrown to the left side in *Cleodora* and to the right in *Pneumodermon*, it (with the branchial cavity) is thrown to the dorsal side in *Limacina* and *Spirialis*. Such a change would be completely paralleled by the arrangement of the parts in the Ascidians, where the first bend of the intestine is dorsal ; but the cloaca, which corresponds to the mantle-cavity, opens on the ventral side, carrying the anus with it ; and even in other Pteropoda we find changes in the arrangement of the mantle-chamber, which to a great extent modify, without, however, essentially altering, the normal arrangement, *e.g.*, in *Hyalæa* and *Cymbulia*, where the posterior extremity of the mantle-chamber extends up to the dorsal surface.

Furthermore, the position of the heart, which remains on the ventral side in *Spirialis* (E. and S., plate 11, p. 13, &c.), greatly strengthens this view of the case.

Leaving this question in abeyance until further light is thrown upon it, we may, I think, enunciate the following propositions with regard to the Pteropoda corresponding to those in which the organization of the Heteropoda was summed up :—

[1] See below, p. 181.

1. The intestine is bent towards the ventral side; the visceral mass is placed above, and in front of the anus; it may be called an abdomen.

2. Some Pteropoda are prosobranchiate, others intermediate, others opisthobranchiate.

3. The foot consists of four parts:—three, the propodium, mesopodium, and metapodium, such as are found in the Heteropoda; and a fourth, the epipodium, not found in the Heteropoda. All of these parts (propodium?) may be distinguished in *Pneumodermon* and *Euribia*, while all but the epipodium and metapodium have disappeared in *Cleodora*.

4. The auditory organs are connected with the pedal ganglia.

5. The Pteropoda are hermaphrodite.[1]

PART II.

The Heteropoda and Pteropoda, whose anatomy I have just endeavoured in a very general way to sketch and illustrate, may be regarded, in some respects, as opposite poles of the development of the archetype of the Cephalous Mollusca. We have now to consider what that archetype is, and by what process it has become modified into the actual forms which have been described; and with the solution of these questions is connected the meaning and justification of certain new terms of which I have made use.

The most proper way of proceeding in this matter would of course be, to trace the *development* of the Heteropoda and Pteropoda. Unfortunately, however, I have had no opportunity of doing this myself; and so far as I am aware, there is no account of the embryogenesis of Mollusks belonging to either of these classes extant.[2]

But in any natural group of animals the grand laws of development and growth are so uniform (the uniformity in fact constituting the true bond of union of its members), that this want may be supplied by the very full information we possess with regard to other Mollusca. If from these data certain general propositions can be established, it will,

[1] This, it will be observed, is here stated for the first time. In the Heteropoda the nature of the generative system has been a matter of controversy, and I therefore gave an account of it at length in *Firoloïdes* and *Atlanta*. The hermaphrodism of the Pteropoda, on the other hand, is well-known, and a description of their generative organs would only have led to details without any morphological bearing.

[2] Since the above paragraph was written, this hiatus has been filled, so far as the Pteropoda are concerned, by Vogt (Bilder aus dem Thierleben, p. 289) and by Johannes Müller (Ueber die Entwickelungs-formen einiger niedern Thiere. Monatsbericht d. k. Akad. zu Berlin, October, 1852.)

I think, be perfectly fair to make these propositions the basis whence deductively to explain and account for facts of organization whose absolute genesis is not known.

The development of the Cephalopoda, Pulmonata, Nudibranchiata, and Tectibranchiata, has been very carefully made out by Kölliker, Van Beneden and Windischmann, Schmidt, Gegenbaur, Sars, Nordmann, Vogt, Reid, and others. From their observations the following generalizations may be safely made.

1. The development of a Mollusk commences on the hæmal[1] side, and spreads round to the neural side, thus reversing the process in Articulata and Vertebrata.

2. In all Mollusks the axis of the body is at first straight, and its parts are arranged symmetrically with regard to a longitudinal vertical plane, just as in a vertebrate or an articulate embryo.[2] Plate V. [Plate 20] fig. 1.

3. The subsequent bent, spiral, or otherwise unsymmetrical arrangement of the parts of the body in Mollusca, depends upon the development of one part at the expense of, or disproportionately to, another ; and this asymmetrical over-development never affects the head or the foot of a Mollusk, but only a portion, or the whole of the hæmal surface. Plate V. [Plate 20] figs. 2-8.

4. It is to this portion, and its often free projecting edges, that we can alone properly apply the term "*mantle*." When this outgrowth takes place before the anus, I propose to call it an *abdomen ;* when it takes place behind the anus, a *post-abdomen.*

5. All embryological evidence goes to show that the Cephalopoda and Pulmonata develope an *abdomen.* The intestine becoming drawn

[1] This very remarkable law has not, it appears to me, received its due importance at the hands of those distinguished anatomists, Kölliker (for the Cephalopoda), Van Beneden, and Windischmann and Gegenbaur (for the Pulmonata), Vogt (for the Nudibranchiata), and Leydig (for the Pectinibranchiata), from whose observations I deduce it. Vogt, however, observes that the order of appearance of organs in the Mollusca is the inverse of that in the Vertebrata ; and with regard to the point from whence development commences, he says, "Ce point est facile de trouver, il est situé en arrière des roues à peu près sur la ligne de jonction entre la partie céphalique et la partie ventrale, et même un peu en arrière de cet dernière sur la partie abdominale même," p. 39.

I use the terms *hæmal* and *neural* here to avoid the ambiguity of dorsal and ventral, which have opposite meanings when applied to the Vertebrata and the Invertebrata. The hæmal side is that upon which the vascular centre is developed, it is the dorsal side of Articulata, the ventral of Vertebrata. The neural side is that upon which the nervous centres are developed ; it is the dorsal side of Vertebrata, the ventral of Invertebrata.

[2] "Instead of the radial type of development we meet quite unmistakably with a lateral symmetrical type ; instead of the extended form of the body we find a short compressed body without repetition of segments or lateral appendages."—R. Leuckart, Morphol. p. 125.

into the abdominal sac becomes in consequence bent towards the neural side. Plate V. [Plate 20] figs. 2-5.

6. On the other hand, all the evidence hitherto obtained with regard to the development of the Nudibranchiata, Tectibranchiata, and Pectinibranchiata, tends to the conclusion, that in them the visceral mass is thrust out *behind* the anus; is in fact a *post-abdomen*.[1] Plate V. [Plate 20] figs. 6-8.

A little consideration will show that the intestine drawn into this must become bent towards the *hæmal side*, as in fact it is in the embryos of all three groups.[2]

Upon embryological grounds, then, we should establish two great primary modifications of the molluscous archetype; the one characterized by the development of an *abdomen*, and a consequent *neural* flexure of the intestine; the other marked by the development of a *post-abdomen*, and the consequent *hæmal* flexure of the intestine.

But these modifications of anatomical structure exactly correspond with those which I have already demonstrated, upon anatomical grounds, to occur in the Pteropoda and Heteropoda; and I trust I am not overstepping the bounds of legitimate analogy in assuming that the anatomical fact of a neural flexure indicates the embryological development of an abdomen; that of a hæmal flexure, the development of a post-abdomen; and that therefore the Pteropoda fall into the same category with the Cephalopoda and Pulmonata; the Heteropoda into that of the Pectinibranchiata, Tectibranchiata, and Nudibranchiata.

It is remarkable that, as regards the flexure of the intestine, similar contrasted modifications of the archetype take place in those animals which are the nearest allies of the Mollusca; I mean the Ascidians and Polyzoa, the Molluscoïdes of Milne-Edwards. In each of these groups the intestine is always bent upon itself; but while in the Ascidian the bend is always *hæmal*, in the Polyzoon it is *neural*. The latter fact is evident to any one who will examine a Polyzoon; the former may seem at first sight to be contradicted by the circumstance, that the ganglion in the Ascidians is placed between the cloacal and

[1] See particularly Leydig, *Ueber Paludina vivipara*, Siebold and Kölliker's Zeitschrift, 1850, where the thrusting forwards of the anus by the development of the mantle is particularly shown, p. 142.

"A considerable change in the position of the anus takes place when the fold of the mantle becomes formed and moves forward, because thereby the intestine and anus are also thrust forward, and to the right side."

[2] The development of the Pectinibranchiata cannot be said to have been carefully worked out yet, with the exception of that of *Paludina*, but what has been done tends to the conclusions above stated.

branchial apertures. However, as I have endeavoured to show elsewhere,[1] whatever be the position of the anus in the Ascidians, the first bend of the intestine is always hæmal. I have already referred to their probable analogy with *Spirialis* in this respect.

Having now determined the changes which take place in the axis of symmetry of the Mollusca, let us examine into those undergone by their principal external organs.

Whether we have to do with a Cephalopod or with an ordinary Mollusk, the first step in development is the separation of the blastoderm into a central elevation, the mantle, and certain lateral portions. Now these portions become in the Gasteropoda, the head and foot ; in the Cephalopoda, the head and arms. It follows, therefore, that the arms of the Cephalopod are homologous with the foot of the Gasteropod.

Again, in the Cephalopod an eminence becomes developed along two lines, which run on each side of the upper part of the "lateral expansions" and meet behind the head ; along the anterior portion of this line the eminence remains as a slight ridge, which afterwards becomes one of the muscles of the funnel ; along the posterior portion of the line a considerable process is developed, and, uniting with its fellow, becomes the funnel.

In the Gasteropod, it is along the *anterior* halves of two corresponding lines that processes are developed, which become the ciliated alæ or vela of the embryo. The line in question I propose to call the *epipodial line*, and whatever is developed along that line I consider to be the epipodium, or a portion of it. I do not venture upon such a refinement at present, but I think it *probable* that, as we have distinguished three portions in the foot, so it will be necessary to distinguish three portions in the epipodium ; anterior, middle, and posterior. For instance, in the Cephalopoda the posterior portion only is developed as the funnel ; in the Gasteropod larvæ the ciliated vela are the homologues of its anterior portion. The palmated lobes of the Turbinidæ, the "lobes of the mantle" of *Aplysia*, appear to be developed from the whole epipodial line, while it is apparently the middle epipodium alone which is developed into the "wings" of the Pteropoda.

All traces of the epipodium appear to have vanished in the majority of the Pectinibranchiata.[2]

[1] Upon the Anatomy and Physiology of *Salpa* and *Pyrosoma*, Philosophical Transactions, 1851, and in a "Report upon the Structure of the Ascidians," read before the British Association, September, 1852. The law as regards the Polyzoa was first enunciated by Professor Allman, "On the Homology of the Organs of the Tunicata and Polyzoa," Trans. Royal Irish Acad. vol. xxii.

[2] Leuckart and Lovén have enunciated very different views with regard to the homologies of the external organs of the Mollusca, to which it seems proper I should refer.

Of all mollusks *Atlanta* possesses the best developed *foot*-proper, and has its parts best specialized and separated. In the special description of *Atlanta* names have been given to these parts, whose appropriateness is, I hope, obvious.

From this highly developed condition of the foot, to its diminished state in *Glaucus* and its total absence in *Phyllirrhoë*, we have every gradation. The various portions are still to be distinguished in *Pteroceras* and the *Strombidæ*, but lose their distinctness for the most part in other Gasteropoda. However, the propodium is still marked off by a transverse fissure in *Oliva* and *Ancillaria*, and attains a great development in size ; a peculiarity which is still more remarkable in

Leuckart, for instance (*op. cit.* pp. 155–59), considers that the anterior cephalic lobes of the embryo Cephalopod answer to the cephalic velum of Gasteropoda ; the posterior cephalic lobes to the alæ of Pteropoda, while the funnel corresponds with the middle lobe of the foot. The arms he considers to be peculiar structures, mere appendages to the cephalic lobes.

If the halves of the funnel, however, answer to the middle lobes of the foot, how is it that they unite upon the dorsal surface of the neck ? If the anterior cephalic lobes answer to the vela of Gasteropoda, how is it that the latter disappear, and do not contribute to the formation of the head in Gasteropoda ? Finally, it must be remembered that the arms of the Cephalopoda arise quite independently of the cephalic lobes, the first developed arms being those most distant from the head.

Leuckart considers that the oral lobes of the pulmonate embryo are the homologues of the ciliated vela of Gasteropoda. But their position and number are against this view. It seems to me that these oral lobes correspond with the cephalic lobes of the embryo Cephalopod, and it has been well shown by Gegenbaur (*op. cit.*) that the whole so-called "yelk-sac" of the Pulmonata is the true homologue of the vela in Pectinibranchiata ; the "ciliated bands" of Van Beneden and Windischmann turn out to be Wolffian bodies, and to be *internal*, not external organs.

The common view, that the alæ of the Pteropoda are the persistent vela of the embryo, is, so far as I am aware, unsupported by any evidence. Embryology teaches us hitherto that the anterior part of the epipodium is never permanently developed, and the position of the alæ would lead to the belief that they correspond to its lateral portions.[1]

So far as I can judge from the Latin table affixed to his Swedish essay on the development of the Acephala, Lovén considers the arms of the Cephalopoda, the three pairs of cephalic tentacles of *Clio*, and the cephalic lobes of *Tethys*, to be homologous with the velum of the Gasteropod embryo, while the funnel of Cephalopoda and the alæ of Pteropoda are homologous with the foot of Gasteropoda.

The considerations above cited appear to me to furnish a sufficient refutation of these views, which seem to be the offspring of an idea first propounded by their learned author in his "Contributions to the Embryology of the Mollusks" (Oken's Isis, 1842), that the hood of *Tethys* and the cephalic processes of *Tergipes* are modifications of the cephalic vela of the embryo. This ingenious hypothesis has not, however, been confirmed by observation so far as regards *Tethys*, and has been directly *dis*proved with respect to *Tergipes* (see Schulze, Ueber die Entwickelung d. *Tergipes lacinulatus*, Wiegmann's Arch. 1849).

[1] The researches of Vogt, already referred to, have fully confirmed this conclusion. The embryo Pteropod has vela, which eventually disappear, while the epipodia are developed quite distinctly from the upper part of the sides of the "foot."

Natica and *Sigaretus*. In both these genera it shows a tendency to invest the head. In the Cephalopoda, the anterior arms, which must be considered as the propodium, fairly unite in front of the mouth, and it seems very possible that the cephalic hood of *Gasteropteron*, the "oral" tentacles of *Aplysia*, the hood of *Tethys*, the "lips" of some Pteropoda, and the hood of *Pneumodermon* may be the result of a similar change. But all attempts to settle these points, save by development, must be more or less hypothetical.[1]

To this same test of development we must refer everything which claims to be called "*mantle*," a word which has perhaps been more vaguely and loosely used than any other term in zoology. Surely if a term is to have any value in either zoological or anatomical nomenclature it must be applied to only a defined thing. The "mantles" of a *Sepia*, a *Cleodora*, or a *Buccinum* may be homologous with one another, but they certainly are not so with what is called the "mantle" in *Doris* or any other Nudibranch.[2] The simple fact that the cephalic tentacles arise in the midst of the so-called "mantle" of the latter, is sufficient evidence to show that it cannot be homologous with the "mantle" of the former. The so-called "margins of the cloak" in these genera appear to me to have much more relation to the epipodium.

Cuvier allows a mantle to *Doris*, but denies it to *Glaucus* and *Eolidia*; why, is not obvious.

Leuckart defines a mantle to be "a scutellate (schildförmig) duplicature of the outer integument extending from the neck for a varying distance backwards." By this definition, however, the upper surface of the anterior division of a *Bulla* would be a "mantle," which it is not, since the true mantle is obviously behind separated from this by

[1] In the absence of any knowledge of development perhaps the source of the nervous supply is one of the best tests of the real homology of a part. Mr. Hancock, in his valuable paper "Upon the Olfactory Apparatus in the *Bullidæ*" (Annals of Nat. Hist., March, 1852), has, I observe, applied this test to the cephalic expansion of the *Bullidæ*, to the hood of *Gasteropteron*, &c.; and since it clearly appears that these parts are supplied by nerves from the *cephalic* ganglia, which never give branches to any portion of the foot, the suggestion in the text must be given up.

[2] Leuckart, believing the hæmal tegument of the Nudibranchiata to represent a mantle, suggests that there is a difference between their "gills" and those of other mollusks, which as he justly observes, are never processes of the mantle, *loc. cit.* p. 130. The argument in the text tends to show, that in this respect there is in reality no difference between the "gills" of the Nudibranchiata and those of other mollusks. On other grounds, however, I am inclined to think that Leuckart's distinction is a just one. The organs called gills in the Nudibranchiata appear to me to be in all cases what they undoubtedly are in *Eolis*, viz., gastro-hepatic appendages. Even in *Doris*, where they are gill-like, they are supplied with hepatic blood only. See Hancock and Embleton's admirable memoir "On the Anatomy of *Doris*," Philosophical Transactions, 1852.

a deep cleft, and how would the mantle of *Firola* or *Carinaroides* answer the definition?

If the definition which I have given of the true "mantle" be correct, we must, I think, hesitate for the present in conferring that name upon the dorsal shell-bearing integument of *Chiton*. May this not be homologous with the thick-edged dorsal surface of a *Doris*, in which the calcareous particles, instead of being scattered, are united into distinct plates?[1]

With regard to the shells, again, at the risk of being blamed for over-refinement, I would suggest that it is, to say the least, an open question whether the shell of *Buccinum* is (as it is commonly supposed to be) homologous with that of *Helix*; that of *Sepia* with that of *Nautilus* and *Ammonites*; that of the embryo *Aplysia* with that of the adult *Aplysia*. Grave differences of development occur in some if not in all of these cases.[2]

From all that has been stated, I think that it is now possible to form a notion of the archetype of the Cephalous Mollusca, and I beg it to be understood that in using this term, I make no reference to any real or imaginary "ideas" upon which animal forms are modelled. All that I mean is the conception of a form embodying the most general propositions that can be affirmed respecting the Cephalous

[1] In D'Orbigny's genus *Villiersia*, allied to *Doris*, the calcareous tegumentary particles of the *Doridæ* have united into a flat shell, hidden in the "mantle," which is pierced by the apertures for the tentacles and gills. The disposition of the calcareous particles in the *Doridæ* is very regular, though it seems too much to assume with Lovén that they imitate a subspiral shell (see Lovén, Oken's Isis, 1842.)

[2] The memoir by Dr. Gegenbaur, "Beiträge zur Entwickelungsgeschichte der Land Gasteropoden," which has just appeared in Siebold and Kölliker's "Zeitschrift für Wissenschaftliche Zoologie," furnishes very powerful support to the doubts above suggested, since it demonstrates that the shell of *Clausilia*, and gives good reason for believing that that of *Helix*, are developed within the substance of the mantle, following exactly the type of *Limax*.

"The land Gasteropoda are distinguished by the peculiar mode of development of their shell, if we may draw conclusions for the whole group from *Helix* and *Clausilia*. The original deposition of the shell in the interior of the mantle (as in the *Loligidæ* among the Cephalopoda) is as yet an isolated fact among the land Gasteropoda, of which we find no indication in other Gasteropods."

There seems to be a very curious relation between the internal or external nature of a shell, the curvature of its whorls as regards a vertical plane, and the hæmal or dorsal flexure of the intestine.

Take, first, the case of a true external shell, as that of *Nautilus* or *Argonauta*, or *Atlanta*. Here the direction in which the shell is wound is the same as that in which the intestine is bent. While the aperture of the shell, therefore, is "hæmad" in *Atlanta* with regard to the axis of columella, it is "neurad" in *Nautilus* and *Argonauta*.

With an internal shell the reverse appears to be the law. Hence the curvature of the shell of *Spirula* is the opposite of that of the shell of *Nautilus*, and that of a pulmonated Gasteropod is the same as that of a Pectinibranch.

Mollusca, standing in the same relation to them as the diagram to a geometrical theorum, and like it, at once imaginary and true.

The archetype of the Cephalous Mollusca then, it may be said, has a bilaterally symmetrical head and body. The latter possesses on its neural surface a peculiar locomotive appendage, the foot; which consists of three portions from before backwards, viz., the propodium, the mesopodium, and the metapodium, and bears upon its lateral surface a peculiar expansion, the epipodium (Plate V. [Plate 20] fig. 1).

The hæmal surface of the archetype may or may not secrete a shell upon its surface or in its interior.

If we compare this unmodified form with the vertebrate or articulate archetype, we find that the three essentially correspond. The appendicular system of the Vertebrata and Articulata is represented by the epipodium in the Cephalous Mollusca (Plate V. [Plate 20] figs. 9, 10, 11).

Nevertheless the differences between the three archetypes are so sharp and marked, as to allow of no real transition between them.

In the Cephalous Mollusca *it is the hæmal side of the body which is first developed.* In the Articulata and Vertebrata it is the *neural side which first makes its appearance.*

The archetype of the Cephalous Mollusca further differs from that of the Vertebrata (and resembles that of the Articulata), in the circumstance, that while in the latter the nervous and intestinal axes are parallel, in the former they decussate; that is, the œsophagus opens on the neural side, passing between the great nervous commissures.

The molluscous archetype again differs from that of both Vertebrata and Articulata in its appendicular system (*ep*), which, when it exists, never presents articulations nor anything that can be called an external or internal skeleton (unless indeed the funnel-cartilages of Cephalopoda be such), and which is generally altogether suppressed in the adult state, its place being supplied by the foot, which, as a development of the central neural region into a locomotive organ, is, so far as I am aware, paralleled throughout the Vertebrata and Articulata by nothing but the dorsal fin of a fish.

In the actual forms, the symmetry of the archetype is almost always disturbed by the excessive development of a peculiar region of the hæmal surface, into what has been termed the abdomen or postabdomen, according as it is placed before or behind the anus.

The integument of this outgrowth, commonly modified in structure and having frequently a prolonged anterior or posterior margin, is the "mantle." It may or may not secrete a shell.

The development of an abdomen (Plate V. [Plate 20] figs. 2, 3, 4, 5)

produces a corresponding *neural* flexure of the intestine, as in Cephalopoda, Pteropoda, and Pulmonata; that of a post-abdomen produces a *hæmal* flexure, as in Heteropoda, Pectinibranchiata, Tectibranchiata, and Nudibranchiata (Plate V. [Plate 20] figs. 6, 7, 8).

From combinations of these primary changes with subsequent greater or less developments of the various parts of the foot, all the varieties of form in the Cephalous Mollusca are produced.[1]

The formation of an abdomen with a peculiar development of the margins of the foot into elongated processes, and with cohesion of the posterior epipodial lobes, gives us the Cephalopodan subtype.

The formation of an abdomen with an excessive development of the epipodium, at the expense of the foot-proper, characterizes the Pteropoda.

The formation of an abdomen with a moderate development of the foot-proper, and hardly any of the epipodium, marks the Pulmonate subtype.

The Heteropoda combine a great development of the foot-proper with the formation of a post-abdomen (and only a transitory development of the epipodium?). The Pectinibranchiata seem to differ from them only in degree.

The development of a post-abdomen, coexistent with that of the epipodium, characterises the Tectibranchiata.

The Nudibranchiata have a post-abdomen and an epipodium in their embryonic condition, but lose both (epipodium?) more or less completely as they attain maturity. The foot-proper is very moderately developed, or even disappears (*Phyllirrhoë*).

If the "mantle" is to have an analogue anywhere among the Articulata or Vertebrata, it may probably be with the carapace of the Crustacea, inasmuch as this is developed from a corresponding region and has similar functions, *i.e.*, to protect the respiratory organs.

Hitherto what has been said has referred to the morphology of the external organs. It remains to show on what plan the internal organs are arranged, and how the archetypal arrangement is modified among the different families. To enter upon this subject fully would belong rather to a formal treatise upon the Mollusca. For the present my object is merely to point out the fundamental unity which obtains among certain of the most important systems of organs, and to bring

[1] For clearness' sake I have referred to the "hæmal" and "neural" flexures as if they always took place in a vertical plane, whereas, as every one knows, the anal aperture is almost always either to the right or the left in the Gasteropoda. The only modification of the theory required to meet this fact, is to suppose that the hæmal outgrowth takes place more rapidly on one side than on the other.

into prominence some facts in the anatomy of the Mollusca which have hitherto been unknown or neglected.

With these views I propose to treat—1, of the nervous system; 2, of the vascular system; 3, of certain portions of the alimentary system; and 4, of the renal system.

1. *Nervous System.*—The nervous sytem of every mollusk consists of two great systems;—A., an excito-motor, or sensory and volitional system; B., a visceral or sympathetic system. The former consists of three pairs of primary ganglia, which always exist, and of a variable number of accessory local ganglia, which may or may not exist.[1]

[1] The first record I can find of the distinct enunciation of this very important anatomical fact, is in M. Souleyet's essay on the Pteropoda (Observations Anatomiques, Physiologiques et Zoologiques sur les Mollusques Ptéropodes), of which an abstract is given in the Comptes Rendus for 1843: he says,—"The central nervous system of the Mollusca is essentially composed of the three orders of ganglia which I have just pointed out (orders answering exactly to those mentioned in the text), and it is in fact reduced to these ganglia in a certain number of animals of this type. But in others the nerves which are given off present numerous enlargements in their course, and this tendency to a ganglionic disposition is so decided among the highest mollusks, that all the nerves emanating from the central medullary masses produce new ganglia in the parts to which they are distributed" (p. 667).

Again:—"From the facts which have just been stated summarily, I believe I may conclude,—

"1. That the exclusive analogy which many naturalists have wished to establish between the nervous system of the Mollusca, and one of the portions of the same system in the animals of higher classes, is not only contrary to physiological principles, but also to anatomical facts.

"2. That the nervous system of mollusks corresponds, in fact, in its distribution to the same parts as those which constitute it in the superior animals, the whole difference consisting in the degree of development and disposition of the parts which is in relation with the rank that mollusks occupy in the series, and the plan which nature has followed in their zoological type.

"3. That the definition very commonly given of this system in mollusks, that it is *composed of ganglia scattered in different parts of the body*, is not exact, since the parts which by their fixity ought to be considered as those which essentially constitute it, are always grouped round the œsophagus. The others, in fact, are to be regarded only as different degrees of development of these central portions, which is proved by their degradation or disappearance in proportion as we descend in animals of this series.

"4. That the central nervous system of Mollusca is always double, and consequently symmetrical, in opposition to what some anatomists have advanced; that it hardly differs in this respect from the nervous system of the Articulata, except by the centralization of the locomotive ganglia, a centralization which may be observed in many animals of the latter type.

"5. Lastly, that it has been wrongly asserted as a general rule, that the ganglia of which the nervous circle of the Mollusca is composed, tend to approximate the higher the organization of the animal, the position of these ganglia being essentially subordinate to that of the organs which they have to innervate" (p. 669).

The very just and admirable views here set forth seem to have met with strange neglect; foreigners, however, might be pardoned for this, since M. Souleyet's own countrymen contrive (see Blanchard, Sur l'Organization des Opisthobranchies, Annales des Sc. Nat. 1848) five years afterwards not to know anything about them.

These three pairs of primary ganglia are the Cephalic, the Pedal, and the Parieto-splanchnic.

I. *The Cephalic Ganglia.*—These are always either in apposition, or are united by a commissure above the œsophagus. They give off either immediately or from the connecting commissure, the following nerves :—

1. Labial, to the lips and anterior parts of the head.
2. Olfactory, to the tentacles.
3. Optic.
4. Buccal, to the buccal mass, tongue, and jaws.

Accessory ganglia may be developed upon all these nerves. They are found upon the labial nerves in *Gasteropteron*, three upon each side (Souleyet and Blanchard) ; upon the olfactory nerves in many Nudibranchiata (Alder and Hancock, Souleyet, &c.) ; upon the optic nerves in Cephalopoda and Heteropoda.

The presence of ganglia upon the buccal nerves is almost constant. There seems to be only one inferior buccal ganglion in some Cephalopoda, while in others there are two, one above and one below. In the Heteropoda, Pteropoda, and most Gasteropoda, there is a pair of ganglia placed laterally at the re-entering angle of the œsophagus and buccal mass. In *Patella*, *Haliotis*, and *Fissurella*, I have found four, two in the latter position, and two anteriorly, just where the buccal nerves come off.

The buccal ganglia are always united by a commissure, so that when the cerebral ganglia are above the œsophagus, an anterior nervous ring is formed ; when they are at the side or below, as in Pteropoda, there is no anterior nervous ring.

II. *The Pedal Ganglia.*—These are either in contact or are united by a commissure ; *below* the œsophagus they give off—

1. Auditory nerves.
2. Pedal nerves.

The auditory nerves are not commonly present, as their organs are generally sessile ; however, they exist in Cephalopoda, and in *Strombus* and *Pterocera*. As has been stated above, the Heteropoda make an extraordinary exception to the usual position of the auditory organs, since in them these nerves appear to be given off from the cephalic

See also the memoir of Hancock and Embleton, before cited, in which the first complete demonstration of the true sympathetic system in the Gasteropoda is given ; and Alder and Hancock's British Nudibranchiata, in which are contained the most beautiful descriptions and figures of the anatomy of the Mollusca extant.

ganglia. Considering, however, that the auditory nerves are invariably attached to the pedal ganglia in all other mollusks, and that in *Pteroceras* and *Strombus*, genera which so nearly approach the Heteropoda, the auditory nerves are very long, I do not think it very hazardous to suppose that in the Heteropoda the auditory nerves really proceed from the pedal ganglia, but have become united to the cephalic ganglia.

In any other case their position is quite exceptional, for the supra-œsophageal position of the auditory sacs in Nudibranchiata merely arises from the pedal ganglia being thrust upwards, and united with the cephalic ganglia.

The accessory ganglia of the pedal ganglion appear to be only what may be called *digital ganglia*, developed to meet the wants of certain elongations or expansions of the foot.

Such are the ganglia at the bases of the arms of the Cephalopoda, and such appear to me to be the ganglia which supply the "labial" processes of *Nautilus*.

III. Under the name of *Parieto-splanchnic system of ganglia*, I include the branchial and visceral ganglia of most authors, and the cervical, branchio-cardiac, and angeial ganglia of M. Blanchard. This system consists of two *primary* ganglia, which are always to be found at the side of the œsophagus, connected with both the pedal and cephalic ganglia, and for which I reserve specially the term *parieto-splanchnic* ganglia ; from these nerves are given off—

1. *Parietal*, to the sides of the body, as distinct from the foot.
2. *Columellar*, to the shell-muscle or muscles, of which there are two in *Octopus*, *Nautilus*, and *Cymbulia* ; one in the shelled Gasteropoda.
3. *Branchial*, to the branchiæ.
4. *Angeial*, to the heart and great vessels and generative organs.

Separate ganglia, answering to the three latter sets of nerves, may be found in the dibranchiate Cephalopoda ; to the two last in the Heteropoda ; a single ganglion corresponding to all of them is found in *Aplysia*, *Buccinum*, *Turbo*, *Paludina*, &c. Two such exist in *Strombus* and *Pteroceras*.

The angeial ganglia, wherever they exist separately, are placed above the aorta and united by a commissure.

The visceral or sympathetic nerves ramify extensively over the intestinal canal (see Hancock and Embleton upon *Doris*). They are connected anteriorly with the buccal ganglia, posteriorly with the parieto-splanchnic system.

To sum up, the typical number of ganglia in the Cephalous Mollusca is three pair, with which accessory ganglia and visceral ganglia may be connected in variable number. The primary ganglia are united by commissures which form—1, two *greater* nervous rings, the *cephalo-pedal*, connecting the cephalic and the pedal ganglia, and the *cephalo-splanchnic*, connecting the cephalic and parieto-splanchnic ganglia: these rings surround both the œsophagus and the aorta. 2, Two *lesser* nervous rings, the cephalo-buccal, uniting the cephalic and buccal ganglia, and encircling the œsophagus, and the parieto-angeial, uniting the parieto-splanchnic and angeial ganglia, and sometimes surrounding the aorta alone: this ring does not seem to be invariably present.

The homology of these ganglia with those of other animals does not, I think, present any very great difficulty.

It is needless to point out their identity with those of the Acephala Lamellibranchiata.

In the Articulata we have corresponding cerebral ganglia, while the subœsophageal ganglionic chain answers to the pedal and parieto-splanchnic ganglia united. The nerves of the latter system appear in a distinct form as the *transverse* nerves of Insects.

It seems possible that the series of lateral ganglia in certain Annelida (*Amphinome*) may correspond with the parieto-splanchnic ganglia of mollusks.

On the other hand, the stomato-gastric nerves with their ganglia in Articulata appear to correspond with the visceral nerves of Mollusca.

To what portions of the nervous system of the Vertebrata do these various ganglia answer? This is a problem which has been variously solved. Unless, with Von Baer, we deny the homology of the centres of the nervous system in the Invertebrata with those of the Vertebrata, an argument whose worth can only be decided by a careful and laborious study of development, it would seem clear that the cerebral ganglia are homologous with the corpora striata and thalami of Vertebrata. Their accessories, the buccal ganglia, answer to the trigeminal ganglia, and supply similar parts.

The cephalo-pedal and cephalo-splanchnic commissures correspond with the crura cerebri; the pedal and parieto-splanchnic ganglia answering to the spinal cord and medulla oblongata. The origin of the auditory nerves would then correspond with that of the seventh pair in Vertebrata, and the pedal nerves with the spinal nerves in function and position.

Again, if the parieto-splanchnic ganglia represent the medulla

oblongata, their branches should, as I think they do, represent a pneumogastric nerve.[1]

Finally the visceral nerves answer to the sympathetic.

The next question to be considered is, in what manner these typical ganglia are arranged and combined to form the almost infinite varieties in the actual nervous systems of the Cephalous Mollusca.

We find—

1. The ganglia concentrated into a mass above the œsophagus, *e.g.*, *Doris*, *Phyllirrhoë*, the majority of the Nudibranchiata.

2. The ganglia concentrated into a mass below the œsophagus, *e.g.*, Pteropoda.

3. The ganglia concentrated around the œsophagus, some above and some below, *e.g.*, *Buccinum*, *Helix*, *Onchidium*, Cephalopoda.

4. The ganglia scattered and separated in pairs, *e.g.*, Heteropoda, Tectibranchiata, and many Pectinibranchiata.

Among these the parieto-splanchnic ganglia may either be united by apposition with the pedal ganglia, and with the cerebral by commissure, as occurs most commonly, *e.g.*, *Octopus*, *Nautilus*, *Haliotis*; or they may be united with the cerebral ganglia by apposition, and with the pedal by commissure, as in *Strombus* and *Pteroceras.*

Patella, *Aplysia*, and *Bullæa* form a gradual transition from one of these conditions to the other.

It will be seen at once from this enumeration that the concentration of the nervous system is by no means a test of high organization in the Mollusca, but rather the reverse.

A peculiarity of the mollusks belonging to the second and third categories, viz., that their infraœsophageal nervous mass is often perforated by the aorta, may be accounted for by the narrowness of the angeial ring, consequent upon the concentration of the elements of the parieto-splanchnic system, so that they unite directly above the aorta.

The singular variation in the arrangement of the different portions of the nervous system, whereby the Mollusca as a class differ so widely from the other great classes of Vertebrata and Articulata, may, I think, find an explanation in the well-known law, that the constancy of a given arrangement of organs greatly depends upon the period at which they appear in embryonic life. If certain organs are formed early, those which come later must obviously accommodate themselves to

[1] Von Siebold compares the nerves which arise between the nerves to the ganglion stellatum in Cephalopoda to a par vagum. Vergl. Anat. p. 379.

their predecessors ; and any variations which have taken place in the latter will perturb the normal disposition of the former.

Now in the Mollusca, as has been already stated, the neural side of the embryo is the last to be developed, and the nervous system does not make its appearance until the animal has taken its characteristic form.

Contrast this with the Vertebrata ; in them the nervous system is the first to be developed, and it is, of consequence, the most fixed and unchanging feature in the whole of their organization.

On the other hand, the separation of the abdomen or post-abdomen from the body is one of the earliest facts in molluscous development, and it has a corresponding influence over their whole organization.

The Archetypal Vascular System and its Modifications.—It may be questioned whether the "archetypal" heart has a single or a double auricle, but it is certain that in proportion as the symmetry of the branchial apparatus and of the whole body is preserved, we approach to the form of heart with a double auricle. Thus we have a double auricle in *Chiton* and *Haliotis*, and a close approach to it in *Tethys*, *Janus*, and the *Eolidæ*.

In the Cephalopoda the contraction of the branchio-cardiac veins has been observed by Milne-Edwards and Kölliker, so that they may be considered to be auricles. This is another curious illustration of the fact, that what is commonly considered the most concentrated and highest organization does not occur in the reputed highest forms of Mollusca.

The heart lies above the intestine, and gives off the aorta anteriorly. This runs forwards through the cephalo-pedal ring with the œsophagus and terminates eventually in the buccal mass. Its main branches may be classed as visceral and pedal.

It is needless to enter here upon the beautiful discoveries of M. Milne-Edwards, with respect to the incompleteness of the circulation in the Mollusca. The facts I have detailed add ocular proof to his already convincing demonstrations. But it is to be observed, that in this respect, again, the "highest" Cephalopod, *Octopus*, possesses no "higher" organization than the Slug or Snail.[1]

The consideration of the archetypal vascular system leads naturally to that of the value of the distinction made by M. Milne-Edwards between *opisthobranchiate* and *prosobranchiate* Mollusca. If my views be well founded, it is clear that opisthobranchism is the typical condition

[1] The "vena cava superior" of Cephalopoda answers to the very short trunk formed by the union of the two afferent branchial trunks in *Aplysia*, &c., which, as receiving the veins of the foot, correspond with the venous circlet at the base of the arms.

of all Mollusks, and that prosobranchism is one result of that asymmetrical development which I have endeavoured to show to be the principal agent in modifying the form of these animals. A little consideration will render it evident, that neither the *neural* nor the *hæmal* flexure will have any effect in altering the position of the heart, so long as the flexure occurs *behind* it, while either flexure will produce prosobranchism, if it take place *before* the heart.

Prosobranchism then indicates that a flexure has taken place, but not in what direction ; opisthobranchism indicates only that no flexure has taken place in front of the heart.

As derived characters, therefore, we may expect them to fail in certain cases ; and those Mollusks which I have chosen to illustrate this paper are instances of their failure. *Firoloïdes* is nearly opisthobranchiate, while *Atlanta* is very decidedly prosobranchiate ; and similar variations, as I have shown, occur among the Pteropoda.

The Archetypal Alimentary Canal consists of—1, lips ; 2, jaws ; 3, buccal mass and tongue ; 4, œsophagus ; 5, crop ; 6, stomach or gizzard ; 7, pyloric appendage ; 8, intestine ; 9, glandular appendages. I wish here merely to draw attention to some peculiarities of the third and the seventh organs in this list, which have not, I think, been hitherto sufficiently noted.

Of the Structure of the Buccal Mass and Tongue (Plate V. [Plate 20] figs. 12, 13, 14, 15).—Although the structure of the "tongue" of the Mollusca has been very elaborately investigated, its mechanism appears to me to have been hardly at all understood.

Cuvier, who first described this structure in *Buccinum*, thought that the buccal cartilages were the chief agents in moving the tongue. He considered the 'tongue-plate' to be passive, and that its movements depended upon the protraction, retraction, divergence, or approximation of the cartilages.[1]

This idea is still further carried out in the Leçons d'Anatomie Comparée (2nd ed. t. v. p. 15–25), where the cartilages are compared to rudimentary jaws, though a little consideration would have shown the jaws to be represented by other organs in some of the instances quoted.

Subsequent writers either coincide in Cuvier's view, or substitute for it some vague notion of licking or rasping ; so Osler[2] and Troschel.[3]

Middendorf, in his elaborate Monograph upon *Chiton* (Malacozoologia Rossica), gives a very careful and detailed description of the buccal apparatus in that Mollusk, but equally fails in rendering its action clear.

[1] Mém. sur les Mollusques, Grand Buccin, p. 9.

[2] Philosophical Transactions, 1832. [3] Wieg. Arch. 1836.

He gives the name of tongue exclusively to a "bifid papillose organ, surrounded by circular folds, which consists mostly of vascular branches, between which masses of muscle are interwoven": this is placed in the floor of the buccal cavity in front of and below the buccal mass.

To what is commonly known as the tongue, he gives the name of "radula," "reibplatte." The dentigerous plate is the "lamina radulæ," its expanded portion the "orbis radulæ." What I have called the buccal cartilages are his "folliculi motores."

It is difficult to come at any clear understanding of Middendorf's views, but so far as I can comprehend them, he appears to consider that the "lamina radulæ" acts as a sort of elastic file pushed from behind by a special muscle, the "curvator radulæ," and supported and steadied by the "folliculi motores."

Von Siebold says,[1] "this organ (the tongue), by its protrusion and retraction, is made use of by the Cephalophora as an ingestive apparatus." He says nothing about the buccal cartilages or the minute structure of the organ.

When I first examined this apparatus carefully six or seven years ago in *Buccinum*, I was convinced that Cuvier had mistaken its mode of operation, and further observation has only strengthened that conviction.

I have already described the manner in which the apparatus may be *seen* working in *Firoloïdes* and *Atlanta*, and I propose now to demonstrate that from the anatomical arrangements the "tongue" has the same chain saw-like mode of operation throughout the Cephalopoda and Gasteropoda. Perhaps *Patella* may be taken as the most convenient illustration, since the organ is here very large, and its parts are distinct and well-developed.

In *Patella* (Plate V. [Plate 20] figs. 12, 13) it is an oblong mass, reddish, except where the tongue-plate shines with a somewhat greenish hue. It is bifid posteriorly, and has a sulcus along two-thirds of its upper surface. In this the tongue lies before it enters the cavity of the mouth. The opening of the œsophagus corresponds with about the anterior fourth of the upper surface of the buccal mass.

To the postero-lateral angles of the mass its extrinsic protractor muscles are attached, two on each side. They go to be inserted into the cephalic parietes, two in front of and above, and two behind the supraœsophageal ganglia. The lower ones are united so as to form a broad muscular plate. Two small muscular bands are also sent from the anterior angles of the buccal mass to the skin of the head.

[1] Vergleichende Anatomie, p. 320.

When the muscular expansion formed by the lower protractors is removed, four or five muscular bands (fig. 12 μ) are perceived inserted by their posterior extremities into the posterior and lower part of the "buccal cartilages," and converging anteriorly to be inserted into the lower edge of an "elastic plate."

From the same point of origin a thick bundle of reddish fibres passes up over the posterior extremity of the cartilages, and is inserted into the upper edge and sides of the "elastic plate." These may be called the intrinsic muscles (fig. 13 μ).

This elastic plate (η) is an elastic transparent membrane, broad posteriorly, and narrower anteriorly, so as to be somewhat heart-shaped. By its superior surface it gives attachment to the "dentigerous plate" (lamina radulæ of Midd.), on which the teeth are set; inferiorly it is very smooth, and plays over the equally smooth pulley-like surface afforded by the larger *buccal cartilages* (fig. 14). These are four in number, two large and two small accessory ones (δ). The larger are elongated, white, cartilaginous-looking plates, excavated internally, and thick and convex behind; their inner edges are kept together by strong transverse muscular fibres. Their upper edges are in contact, forming the smooth surface mentioned above; the smaller seemed to be in a manner sesamoid cartilages; they are connected anteriorly with the tongue-plate and posteriorly with muscular fibres, which are inserted into the larger cartilages.

It is clear that the action of the intrinsic muscular bands (having the insertions described) must be to cause the "elastic plate," and with it the "dentigerous plate," to traverse over the ends of the cartilages, just like a band over its pulley, the cartilages themselves being entirely passive in the matter. The extrinsic bands, again, must serve to protract the whole mass and thrust it more or less firmly against the object to be acted upon.

I have examined *Buccinum*, *Fissurella*, *Doris*,[1] *Aplysia*, *Bullæa*, *Helix*, *Onchidium*, *Cypræa*, *Pteroceras*, *Sigaretus*, and *Vermetus*, and in all I have found a structure essentially similar to that here described; the difference consisting in the greater or less length of the dentigerous plate, and the more or less complete development and isolation of the buccal cartilages. These are the less distinct the more the tongue becomes a mere organ of deglutition. *Aplysia* and *Bullæa*, for instance, have the cartilages united and much softer than in most genera. The structure of the Cephalopod tongue closely resembles that of *Aplysia;* and it has the further peculiarity, that the portion of

[1] See also the description of the "tongue" in this genus by Messrs. Hancock and Embleton, *loc. cit.* p. 210.

the floor of the buccal cavity in front of the tongue (true tongue of Middendorf), which is plicated and distinct in most Gasteropods,[1] is in the Cephalopods raised up into a laminated caruncle (or several) larger than the tongue itself.[2]

This pulley-like structure of the tongue appears to me to be very characteristic of the portion of the molluscous type here considered,[3] and indeed to be peculiar to it. Its occurrence in *Chiton*, therefore, would effectually determine the molluscous nature of that genus, even if there were no other grounds for the conclusion ; while the structure of the buccal armature of *Sagitta*, which has been compared to the protruded tongue of a Heteropod, is, in fact, so totally different as at once to remove it from the Mollusca.[4]

I may further remark, that the structure of the tongue in the Cephalopoda adds one more link to the very strong chain of affinity between them and the ordinary Mollusca.

Of the Pyloric Sac.—This appears in various forms in a great number of the Mollusca, and seems to be always in special relation with the liver. In *Atlanta* it has been seen that its glandular parietes form the liver. In the Cephalopoda the hepatic ducts enter its representative, the spiral sac of *Octopoda*, the elongated sac of *Loligo*. The extreme length of the pyloric sac in *Cleodora*, and the occurrence of a second smaller one, appear to be leading the way to the ramified prolongations of the intestinal canal found in the *Eolidæ*.

In *Pteroceras* a very remarkable structure exists, which, so far as I am aware, has not yet been noticed.[5] The existence of a " crystalline

[1] Osler, *loc. cit.* p. 505, describes a soft striated papilla arising from the floor of the mouth in front of the tongue in *Patella*, which, he says, " is probably the organ of taste."

[2] See Owen, Article ' Cephalopoda,' Cyc. Anat. and Phys. Is the " horny striated substance " supporting the lingual teeth, " which appears to represent the body of an os hyoides " in *Nautilus*, the representative of the buccal cartilages?

[3] It has been noticed by Troschel (Anatomie von *Ampullaria Urceus*, Wieg. Arch. 1845), that the structure of the tongue is the same throughout those Mollusks which have a head : " Under the jaw lies the anterior part of the so-called tongue, a membrane which is present in all Pteropoda, Cephalopoda, Gasteropoda, in short, in all those Mollusks which possess a head. It is wanting in all the so-called Acephala, in the Bivalves, and in the Tunicata. It rests, as in all cases where it is present, upon two portions of cartilage of whitish colour combined by a membrane and moved by many muscles." It is clear, however, from this passage, that Troschel has not recognized the true mechanism of the organ.

[4] There is a curious similarity between the " tongue " of the Mollusca and the arrangement of the dental apparatus in the Plagiostome fishes, which may be viewed perhaps as another illustration of Von Baer's law, that while the exterior of a vertebrate animal is Articulate in its construction, the interior is Molluscous.

[5] Since writing the above, I find that so far back as 1829, the existence of this organ was distinctly pointed out, though strangely enough the fact has been quite overlooked by every one save Von Siebold ; he, however, merely refers to the statement in a note, and

style" in connection with the alimentary canal, has long been known in the Lamellibranchiata, but it has hitherto been supposed to be confined to them. However, in *Pterocerns*, the pyloric sac contains a very complete style, Plate V. [Plate 20] figs. 16, 17.

The stomach is a wide somewhat quadrangular cavity. The œsophagus opens into its left anterior angle, while its pyloric orifice, very close to this, is at the right anterior angle. Behind the pyloric orifice the rounded head of the crystalline style projects from the aperture of the pyloric sac, γ, fig. 16.

Two wide apertures communicate with the liver, and act as hepatic ducts.

Several considerable ridges of the gastric membrane rise from the floor of the stomach ; the principal one is next to the cardia, and there is a smaller between the cardia and pylorus. The aperture of the pyloric sac is surrounded by an elevated circular ridge, which is slit towards the pylorus, the left edge of the slit overlapping the right. The end of the style projecting from this orifice is opposed by one or two cartilaginous plates upon the principal elevation. It is only the end of the style which is free ; for the rest of its length (two or three inches) it lies in the pyloric sac (λ, fig. 17), which runs back over the intestine, in the thickness of the left side of the mantle, and terminates by a rounded extremity.

It seems probable that the "crystalline style" is secreted by the pyloric sac, and that it acts as a gastric plate, assisting in the comminution of the food, although its transparent and delicate texture would not seem to fit it for the performance of any very important office of this kind.

Its resemblance in position and structure to the crystalline style of *Solen* is sufficiently remarkable.

Renal System.—It has been shown that in the Heteropoda and Pteropoda a "contractile sac" exists, placed so as to be bathed by the blood entering the auricle. It has been hinted that this is a renal organ, and I now proceed to give the reasons for my belief that it is so.

says he "does not know what to make of it." (Vergleichende Anatomie, p. 312.) This statement is contained in a valuable paper upon the anatomy of the Mollusca, entitled "General Observations on Univalves," by Mr. Charles Collier, Staff-Surgeon at Ceylon ; printed in the Edinburgh New Philosophical Journal for 1829, p. 231. "There is an organ, the crystalline stiletto, confined erroneously by a celebrated naturalist (Cuvier) to bivalves, which is found in every species of *Strombus*, in *Trochus turritus*, and a species (*Vertagus*) of *Murex*. It is enclosed in a sheath, that passes parallel to and by the side of the œsophagus, to the stomach, into which the stiletto enters, leaving its covering ; that end which lies within the stomach is obtuse, laminated, and fixed by a hook of similar substance to its situation. The upper portion is circular, homogeneous, slightly tapering, transparent, of gelatinous consistence, and resembling somewhat a pistil with its stigma."

A hollow sacculated organ, with yellowish glandular parietes, surrounds the base of the pulmonary sac in the Pulmonata, and opens by the side of the rectum. The secretion of this organ has been shown to contain uric acid.[1] No contractions have been observed in it.

In *Fusus*, *Cypræa*, and other Pectinibranchiata, an aperture, frequently seated upon a kind of papilla placed at the posterior and upper part of the branchial chamber, leads into a wide cavity, which is in relation above with the pericardium, and on the sides with the rectum and generative duct. In its anterior wall a yellow gland is frequently attached, which consists of large vascular laminæ. I observed no contractions of either the sac or the yellow gland, but my attention was not at the time particularly directed to this point.

Now I think that this sac, with its vascular gland, is exactly comparable in position to the "contractile sac" and to the renal organ of *Pulmonata*, while, on the other hand, it closely resembles the serous chambers with their contained venous appendages, which open into the mantle-chamber of the Cephalopoda.

The venous appendages of the Cephalopoda, however, have been demonstrated to be renal organs by containing secreted uric acid, and they possess the faculty of rhythmical contraction.[2]

The chambers of the venous appendages, then, in the Cephalopoda answer to a "contractile sac," in which the secreting power and the contractile faculty have become restricted and localized in a portion of the organ.[3]

I have here touched mainly upon the less commonly understood portions of the internal anatomy of the Cephalopoda and Gasteropoda, but they clearly tend to strengthen the conclusion to be derived from embryology and the more generally known anatomical facts, viz., that the Cephalopoda and Gasteropoda are morphologically one, are modifications of the same archetypal molluscous form.

On the other hand, I have made no reference to the Acephala, nor is it my intention to go into that part of the subject ; but, for the sake of the zoological bearings of the question, I may shortly express my belief, that of the two families of the Acephala, there is abundant evidence, both anatomical and embryological, to show that the one,

[1] H. Meckel, Müller's Archiv, 1846.

[2] Kölliker, Entwickelungsgeschichte d. Cephalopoden.

[3] A renal organ of similar character has been long since demonstrated in the Lamellibranchiata. (See Von Siebold, Vergl. Anat.)

the Lamellibranchiata,[1] is modelled upon the archetype of the Cephalous Mollusca.

Such evidence as we possess with regard to the Brachiopoda, however, is purely anatomical, and (though I am aware that a great weight of authority lies upon the other side) yet Mr. Hancock's opinion, that they are rather to be considered as allied to the Polyzoa than to the Cephalous Mollusca, seems to be quite as plausible as the more general notion.

Should this highly ingenious suggestion be found by embryology to be correct, the Brachiopoda will have the same relation to the Polyzoa as the simple Ascidians to the compound Ascidians, and will form a parallel group to the former in M. Milne-Edwards's section of "*Molluscoïdes.*"

In conclusion, I would observe that the archetypal Cephalous Mollusk (as thus defined) is, in all its modifications, sharply separated from other archetypes, whatever apparent resemblances or transitions may exist. In all cases these will, I believe, on close examination, be found to be mere cases of analogy, not of affinity.

As Cuvier long ago remarked of the Cephalopoda and Fishes, so we may say of the Cephalous Mollusca in general and other types :— "Whatever Bonnet and his followers may say, Nature here leaves a manifest hiatus among her productions." For instance, great as are the apparent resemblances between a Lamellibranch and an Ascidian, they all vanish upon closer examination.[2] Neither in its anatomical nor in its embryological relations does the branchial sac of an Ascidian correspond with the mantle-cavity of a Lamellibranch.

The nervous system is totally different. The three pairs of ganglia, which exist in all Lamellibranchiata (even the apodal genera), are replaced by one in the Ascidians, which is not homologous (as is commonly asserted) with the branchial ganglion, or intersiphonic ganglion of Lamellibranchiata, but with their pedal ganglion.

The organization of the circulatory system is wholly different. The

[1] The Lamellibranchiata are as truly cephalous as many Pteropoda, and the possession of a distinct head is so much a question of degree as to be a very unfit classificatory character.

[2] I beg that I may not be misunderstood here. While I consider that there is no transition between the Cephalous Mollusca as such, and the Ascidians or Polyzoa, I also fully believe (and so far as the Ascidians are concerned I have endeavoured to demonstrate, Report on the Structure of the Ascidians, already referred to) that the archetype of the Cephalous Mollusca, that of the Ascidians and that of the Polyzoa, are all referable to a common archetype, the archetype of the Mollusca generally. It is one thing to believe that certain natural groups have one definite archetype or primitive form upon which they are all modelled ; another, to imagine that there exist any transitional forms between them.

Every one knows that Birds and Fishes are modifications of the one vertebrate archetype ; no one believes that there are any transitional forms between Birds and Fishes.

Ascidians have a cellulose test, not a calcareous shell. The larval conditions are totally distinct.

If, however, all Cephalous Mollusks, *i.e.*, all Cephalopoda, Gasteropoda, and Lamellibranchiata, be only modifications by excess or defect of the parts of a definite archetype, then, I think, it follows as a necessary consequence that no anamorphism takes place in this group. There is no progression from a lower to a higher type, but merely a more or less complete evolution of one type.

It may indeed be a matter of very grave consideration whether true anamorphosis ever occurs in the whole animal kingdom. If it do, then the doctrine that every natural group is organized after a definite archetype, a doctrine which seems to me as important for zoology as the theory of definite proportions for chemistry, must be given up.

DESCRIPTION OF THE PLATES.

In all the Plates the same letters refer to the same parts.

a. Anus.
b. Buccal mass.
c. Contractile sac.
d. Subspiral ciliated band.
ep. Epipodium.
f. Salivary gland.
g. Tentacles.
h. Head.
i. Eye or optic nerve.
j. Auditory vesicle or nerve.
k. Stomach.
k'. Pyloric cæcum.
l. Liver.
m. Mantle.
mt. Metapodium.
ms. Mesopodium.
n. Branchiæ.
o. Ovary.
p. Penis.
pp. Propodium.
q. Abdomen.
r. Post-abdomen.
s. Vesicula seminalis.
t. Testis.
u. Auricle.
u'. Venous canal.
v. Ventricle.
w. Aorta.
w'. Recurrent artery.
x. Cerebral ganglia.
y. Pedal ganglia.
y'. Pedal artery.
z. Parieto-splanchnic ganglia.

β. Buccal ganglia or nerves.
γ. Crystalline style.
λ. Its sheath.
δ. Accessory cartilages of the buccal mass.
θ. Tongue plate.
η. Elastic plate.
μ. Muscles.

PL. II. [Plate 17]

Fig. 1. *Firoloïdes Desmarestii.* (Magnified.) Male.
Fig. 2. *Firoloïdes Desmarestii.* Female. Posterior extremity from the left side.
Fig. 3. *Firoloïdes Desmarestii.* Female. Posterior extremity from the right side.
Fig. 4. Penis of the male.
Fig. 5. Egg-tube.

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Fig. 1

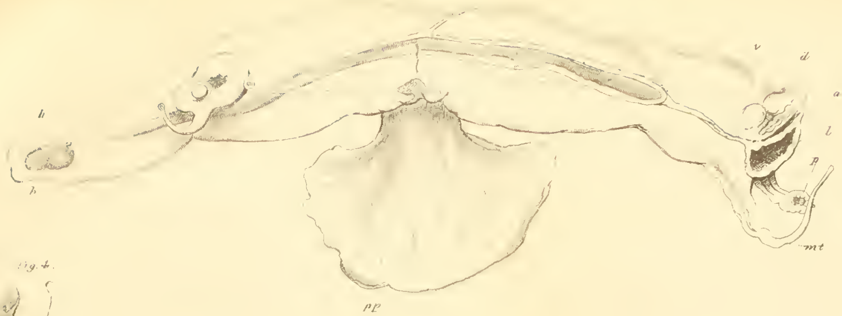

Fig. 4.

Fig. 2

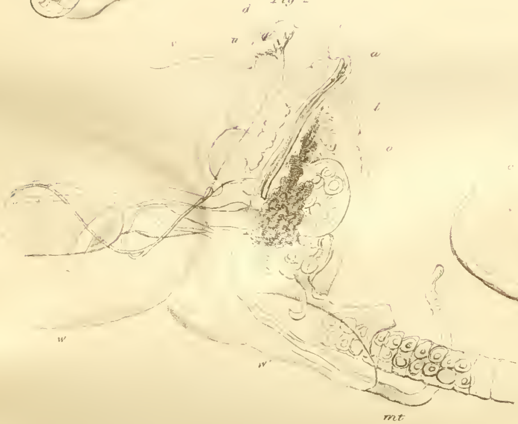

Fig. 3.

Fig. 5.

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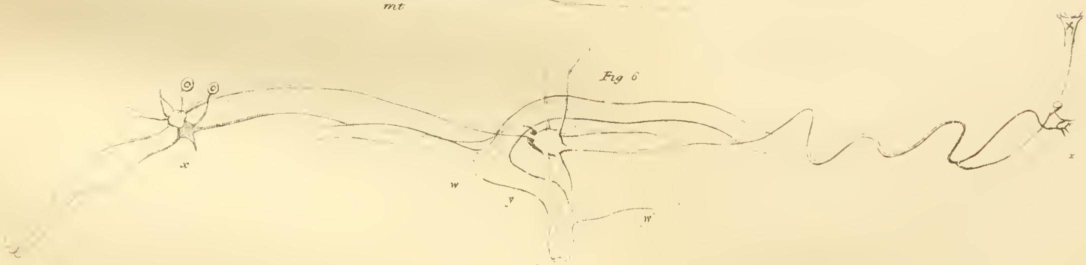

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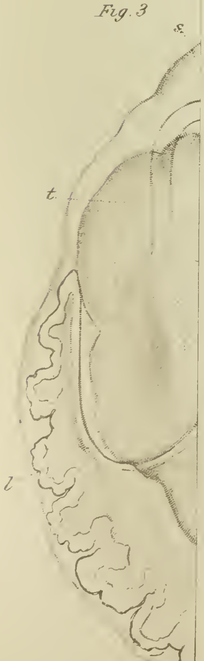
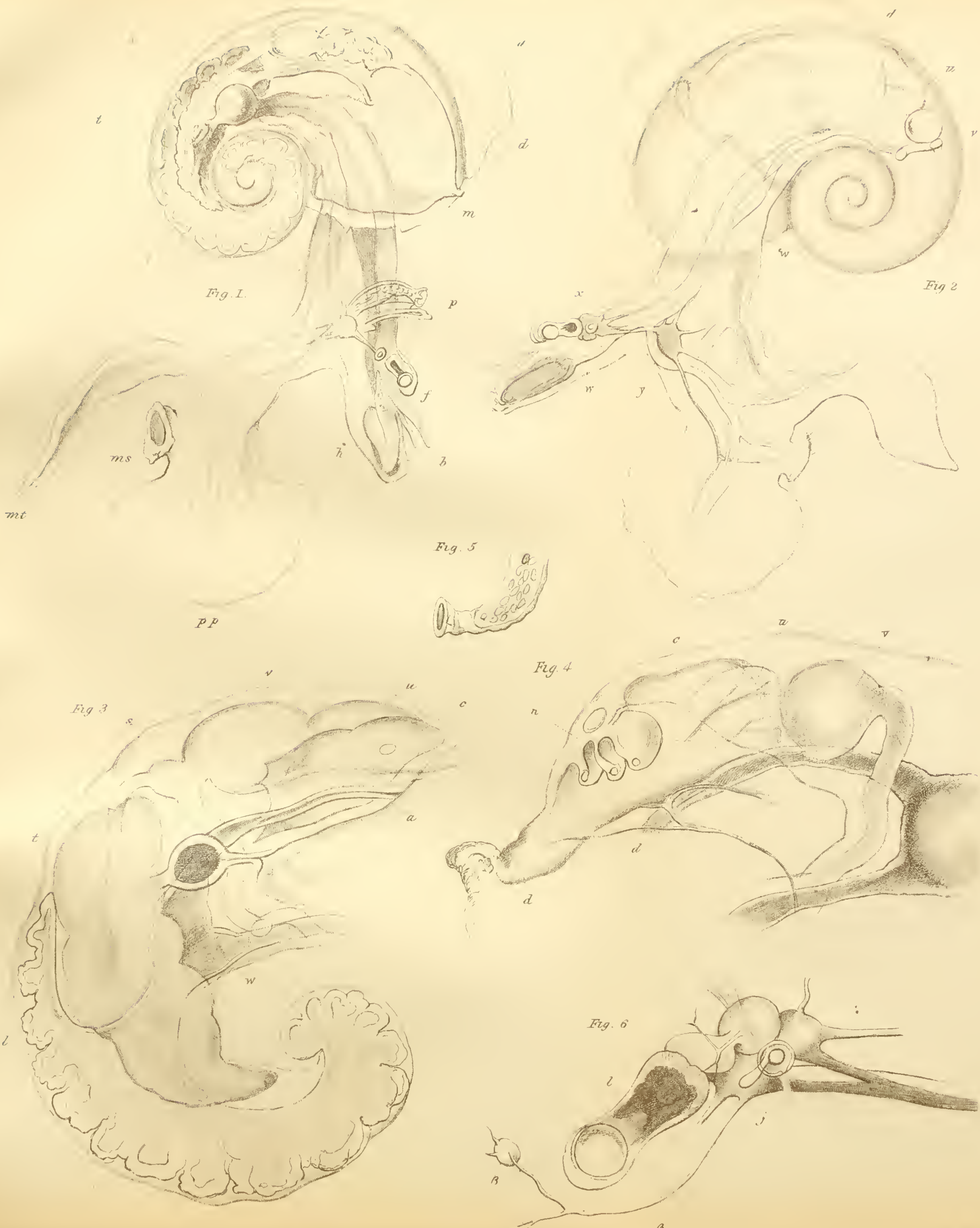
Fig. 8

Fig. 3





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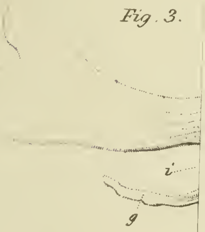

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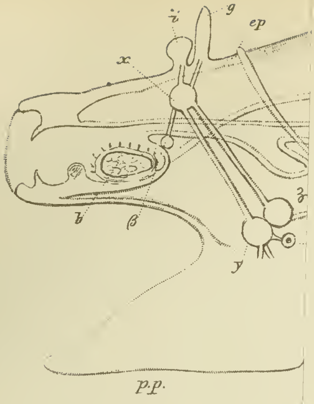

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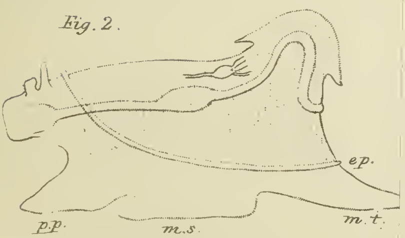

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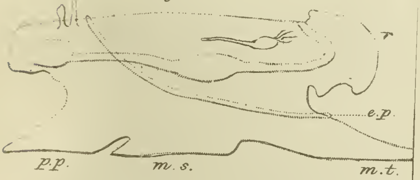

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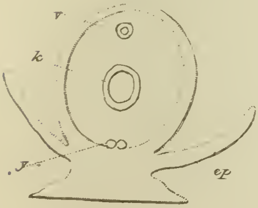

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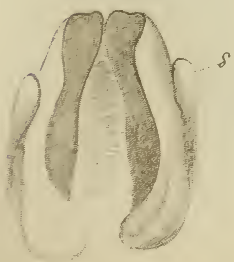

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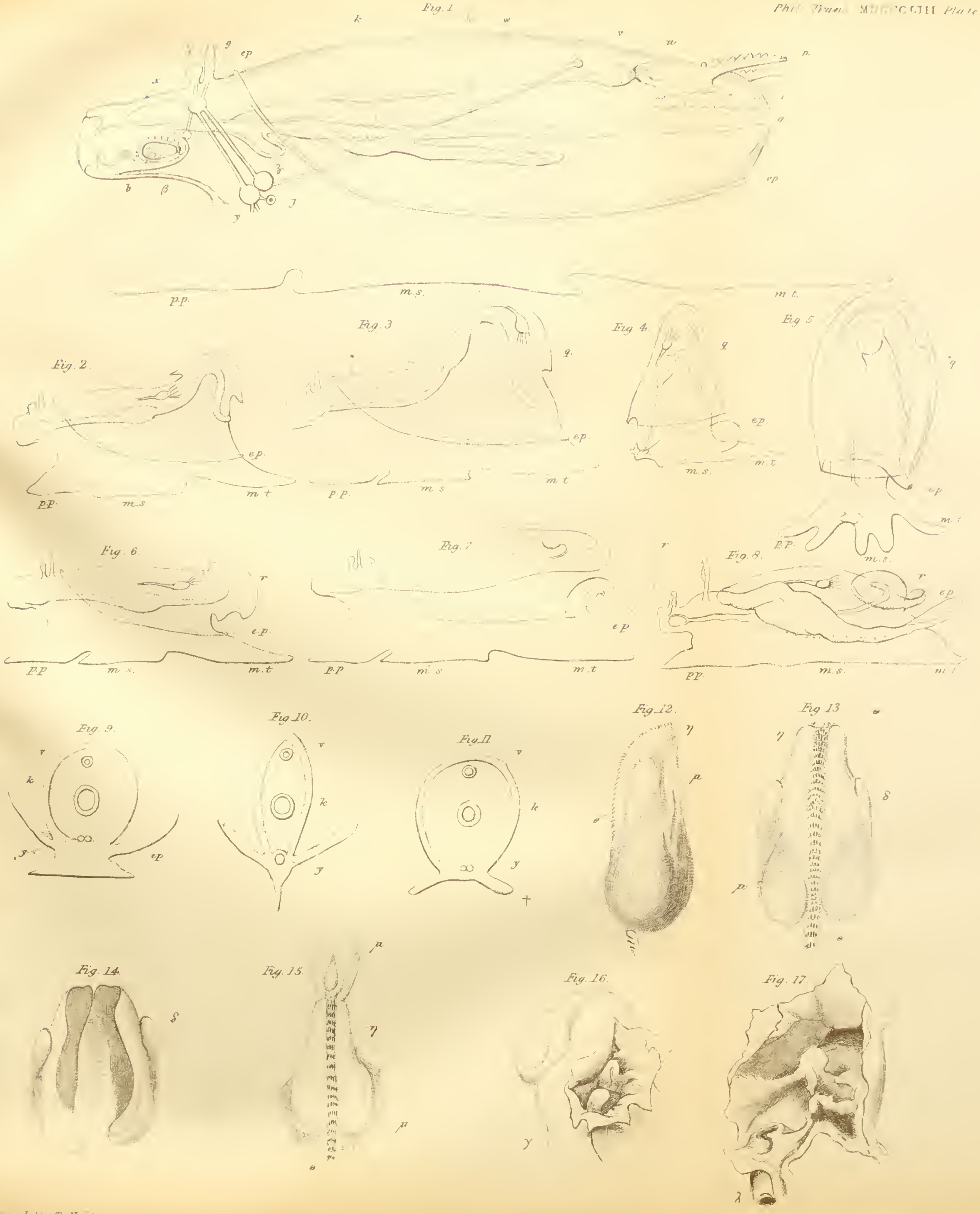
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Fig. 6. Nervous system, with the termination of the pedal artery at *y'*.
Fig. 7. Cerebral ganglia from below.
Fig. 8. Right eye and tentacle.

PL. III. [Plate 18] ATLANTA LESUERII.

Fig. 1. Animal in its shell (much magnified), from the right side. Male.
Fig. 2. The same from the left side, to show the arrangement of the nervous and vascular systems.
Fig. 3. Post-abdomen, without the shell; more enlarged, from the right side.
Fig. 4. Portion of the mantle-cavity and post-abdomen from the left side, to show the arrangement of the heart and branchiæ.
Fig. 5. Portion of the penis.
Fig. 6. Cerebral ganglia, from the left side.

PL. IV. [Plate 19]

Fig. 1. *Pneumodermon* ——— ? A young specimen, to show the form of the foot and its relations.
Fig. 2. *Euribia Gaudichaudii* (Eydoux and Souleyet), from behind, placed, not as it swims, but so as to leave its parts in their normal position. This has been done with each of the figures in this Plate, except it be otherwise expressly mentioned.
Fig. 3. The head and foot of *Euribia*, seen from below.
Fig. 4. *Cleodora curvata* (Eydoux and Souleyet), from the neural side.
Fig. 5. The same, from the hæmal side.
Fig. 6. *Cleodora aciculata*, from the right side, without the shell.
Fig. 7. The same. The head and alæ from the neural side.

PL. V. [Plate 20]

The first eleven figures are to be regarded as mere diagrams, illustrative of the archetypal form of the Mollusca and its more important modifications.

The shaded portion is the hæmal surface, the unshaded the neural surface.

Figs. 2 and 3 are supposed to represent the development of an abdomen, and the changes of position thence undergone by the intestine and heart.
Fig. 4 is a diagram of a Pteropod, corresponding with fig. 2.
Fig. 5 is a diagram of a Cephalopod, corresponding with fig. 3; but in these, changes in the different parts of the foot have been also effected.
Figs. 6 and 7, similarly are supposed to represent the development of a post-abdomen.
Fig. 8. A diagram of *Aplysia*, corresponding with fig. 6. *Atlanta* corresponds exactly with fig. 7.
Figs. 9, 10, 11, are imaginary sections of a Mollusk, a Fish, and an articulate animal, respectively, to show the relations of the nervous, alimentary, vascular, and appendicular systems.

The Mollusk and articulate animal are in their normal position; the fish is turned upon its back to correspond with them. * The pectoral fins. † The legs of the articulate animal.

Figs. 12–15. The buccal apparatus or tongue of *Patella*.
Fig. 12. From the right side.
Fig. 13. From above.
Fig. 14. The supporting cartilages.
Fig. 15. The elastic plate which plays over them.
Figs. 16, 17. The stomach of *Pteroceras*.

XVIII

RESEARCHES INTO THE STRUCTURE OF THE ASCIDIANS

British Association Report, 1852, *pt.* 2, *pp.* 76–77.

THE author stated that he was desirous of laying before the Section an account of some investigations into the structure of the Ascidians which he had been led to make while endeavouring to form a catalogue of those contained in the collection of the British Museum.

The Ascidians, varied as they are in external appearance, present certain general anatomical uniformities, which are capable of being represented by a diagram. To such a hypothetical structure thus represented, the author gives the name of the Archetypal Ascidian. From this every actual form can be shown to be derived, by very simple laws of modification. The author particularly desired it to be understood that he attached no other meaning to the term Archetype than that thus defined.

It has been a matter of dispute which is the dorsal and which the ventral side of the Ascidians; there can be no question, however, that the heart is upon one side of the axis of the body, and that the nervous ganglion is upon the other; to avoid all ambiguity, therefore, the author proposes to speak of the "hæmal" and of the "neural" sides, in accordance with the nomenclature proposed by him in a memoir 'Upon the Homologies of the Mollusca,' read before the Royal Society. The Ascidian Archetype differs from all others in the following points:

1. The intestine is always flexed towards the hæmal side. In the Polyzoa it is flexed towards the neural side, as pointed out by Professor Allman.

2. The tentacles are small, while the pharynx is very large, and serves as a respiratory cavity, its parietes becoming perforated. The author combated the view that the "branchial sac" of the Ascidian answers to the tentacles of the Polyzoon, or to the united gills of the

Lamellibranchiate Mollusk; in opposition to the former view, he endeavoured to show that the tentacles of the Polyzoa are represented by the tentacles of the Ascidians; and against the latter, he urged, that the gills of the Bivalve Mollusk have no representative in the Ascidian. The "branchial sac" of the latter, represents not the gills of the Mollusk, but the perforated pharynx of Amphioxus; an analogy which has already been noticed by many observers.

The author brought forward the structure of the peculiar genus *Appendicularia*, as fatal to the view that the branchial sac of the Ascidian is homologous with the united tentacles of the Polyzoa.

Especial attention was directed to the formation of what the author termed the "Atrium," under which term he included the cloaca and the space between the branchial sac and the "third tunic" of writers. The author endeavoured to show that it answers to the mantle-cavity of ordinary Mollusks; that its excessive development accounts for the presence of the "third tunic" in the Ascidian, and that Savigny's comparison of an Ascidian to an inverted Patella had very considerable justice.

The author next proceeded to detail many structural points of interest which he had made out in the genera examined. A minute account was given of the structure of the branchial sac in *Boltenia*, *Cynthia*, *Phallusia*, *Syntethys*, and other genera. The branchial meshes are always true apertures, generally more or less rectangular or oval in shape; but in one species described they were arcuated or semilunar, so as to give the appearance of spiral vessels in the branchial tissue.

The structure of the dorsal folds and of the "Endostyle," a structure first noticed as distinct by the author in his memoir upon the *Salpæ*, was minutely described; and the singular and characteristic variations in form of the peculiar organ of sense—the "tubercule antèrieure" of Savigny—were pointed out.

The "Tubular System," described in the same memoir as a peculiar and unique organ in *Salpa* and *Pyrosoma*, was shown to be the form of hepatic organ proper to, and universal among the Ascidians.

The reproductive system exhibits remarkable and hitherto little noticed peculiarities, which have led the author to distinguish the simple Ascidians into Monothalamous and Dithalamous groups, the section Styela (Sav.) being the type of the latter. Owing to the discovery of a *Marsupial* Cynthia, that is, of one whose ova pass through all stages of their development in the Atrium of the parent, the author was enabled to lay some interesting embryological facts before the

Section. The Cynthia in question has the appearance of a compound form ; it does not, however, become multiplied by gemmation like the true compound forms, but the originally free, tailed larvæ, adhere and become firmly united before the withering away of their appendages. The mass is therefore an aggregation of distinct individuals, not one individual represented by many Zöoid forms.

The development of the muscular tissue of the tail was described, closely resembling that of the muscles of the tadpole as given by Kölliker.

With respect to the structure of the test of the Ascidians, the author stated that he had verified in many new cases the discovery of the presence of cellulose in large quantities therein made by Schmidt, and extended by Löwig and Kölliker, and by Schacht. In other points, the author's results differed somewhat from those of these writers ; and after pointing out what he considered to be the true structure, he drew particular attention to the essential identity of the test of the Ascidian with true bone (if for the calcareous salts cellulose be substituted) on the one hand, and with vegetable tissue on the other. The physiological distinction between plants and animals, which authors have endeavoured to draw, upon the ground that the Ascidians do not *form* cellulose, but only take it from plants, seems incompatible with the circumstance made out by the author, that the Ascidian larvæ contain cellulose while they are yet a mere mass of cells contained within a structureless membrane, and totally without any organ, except the tail.

The author endeavoured to show that the Ascidians might be divided into natural groups, by considering :—

1st, The arrangement of the organs with regard to the axis, whence the animal may be symmetrical or asymmetrical, according to the relative development of the neural and hæmal regions, and of the branchial sac ; and,

2ndly, The nature of the tentacles and of the reproductive organs.

In conclusion, the author stated that the Ascidian type appeared to be sharply defined from all others, nowhere exhibiting any transition forms.

XIX

ON THE ANATOMY AND DEVELOPMENT OF ECHINOCOCCUS VETERINORUM.

Zoological Society's Proceedings, vol. xx. 1852, *pp.* 110–126
(*Pl. XXVIII.–XXIX.* [*Pl.* 21, 22]).

On the 25th of November, 1852, a fine female Zebra, whilst at play within its paddock, accidentally broke its neck. The animal had always appeared to be quite healthy, and it was in perfectly good condition—but, upon examination, its liver was found to be one mass of cysts, varying in size from a child's head downwards. The liver was taken out of the body on the day succeeding the animal's death[1] —and on the 27th I proceeded to examine the contents of one of the largest cysts (with a portion of its wall) and one of the smaller cysts.

It was at once obvious that the cysts contained the *Echinococcus veterinorum*, and I may here mention that the *Echinococci* were in full life, and remained so for three days, until, in fact, the fluid in which they were contained had become slightly offensive.

It will conduce to clearness, perhaps, if I state in successive order I. What I saw myself. II. The theory of the formation of the *Echinococcus*-cysts, and of their relation to other forms of Entozoa, which I have to offer. III. What has been done hitherto.

I. The cysts are nearly spherical vesicles having a very elastic proper wall; so elastic, in fact, as to exercise a continual tension upon the contained fluid, which, if the cyst be pierced, spurts out in a jet for some time.

The outermost layer of the cyst is an adventitious membrane, formed by the infested animal around the *Echinococcus*-cyst, as it would be developed round any other foreign body; with this I have nothing to do. Within this, and in nowise adherent to it, follows the proper wall of the *Echinococcus*-cyst, which must be carefully

[1] I beg here to express my obligations to the Secretary of the Zoological Society, without whose kind recollection of a wish to examine fresh Entozoa, which I had expressed, I should not have had the opportunity of making the observations contained in the present paper.

distinguished into two portions. The outer is thick, yellowish and constituted by a great number of delicate, structureless laminæ composed of a substance closely resembling Chitin. It is to this laminated membrane that the elasticity of the cysts is due—and it must be regarded as precisely analogous to those structureless cysts which surround the pupa forms of *Distomata* imbedded in the body of snails, or to those similarly structureless cysts which enclose the encysted *Tetrarhynchi*, and which Van Beneden saw in course of formation by a process of exudation, around the Scolex form of those worms. The innermost layer of this, which, for distinction's sake, I will call the *Ectocyst*, is whiter and softer than the others, and appears to be in course of formation.

The inner portion of the wall of the *Echinococcus*-cyst is closely adherent to the last described layer of the ectocyst, but may, with great care, be separated from it, when it is at once evident that there is no organic connexion between the two; this layer may be very conveniently termed the *endocyst*—it is the only active living part of the whole wall of the cyst, and represents the proper body-wall of the animal. It is very pale and delicate, and not more than $\frac{1}{2000}$th of an inch thick (Pl. XXVIII. [Plate 21] fig. 5). It is composed of very delicate cells $\frac{1}{2000}-\frac{1}{5000}$th of an inch in diameter, without obvious nuclei, but often containing clear, strongly refracting corpuscles, generally a single one only, in a cell. These corpuscles appear to be solid, but by the action of dilute acetic acid, the interior generally clears up very rapidly, and a hollow vesicle is left of the same size as the original corpuscle. *No gas is developed during this process*, and sometimes the corpuscles are not acted upon at all by the acid, appearing then to be of a fatty nature. A strong solution of caustic ammonia produces a concentrically laminated or fissured appearance in them. Under pressure, and with commencing putrefaction, a number of them sometimes flow together into an irregular or rounded mass.

The inner surface of the endocyst is sometimes irregularly papillated like a glandular epithelium in consequence of the prominence of separate cells (Pl. XXVIII. [Plate 21] fig. 5), or its surface presents an even contour, from the presence of a structureless membrane, which varies in thickness, and seems to represent the inner portion of the blastema, elsewhere slightly granular, in which the cells are imbedded (Pl. XXVIII. [Plate 21] fig. 2).

Solitary hooks are scattered over the inner surface of the endocyst. I thought at first that they had fallen from the *Echinococci*; but it is with some difficulty that, even by the aid of pressure, the hooks can be so detached from them; and furthermore the hooks in question

had generally the appearance of those forms found in the younger *Echinococci*, from which there is still greater difficulty in detaching them. I conclude then that these hooks are developed where they are found, and that they represent a sort of attempt to develope an *Echinococcus* which has gone no further. Within the substance of the endocyst one may see here and there traces of clear delicate vessels, such as those which will be described in the secondary cysts; but probably in consequence of the granular nature of the membrane, they are rarely visible.

In describing the development of the *Echinococci*, it will be necessary to return to this endocyst—at present I pass to the contents of the cyst. This is a clear, colourless, serous liquid, in which two kinds of bodies are found floating, *a. Echinococci*, and *b.* secondary cysts.

a. Echinococci (Pl. XXVIII. [Plate 21] fig. 1.) To avoid circumlocution, I restrict this term in the present place to what are commonly called the *Echinococcus*-heads.

The *Echinococci* are minute, oval bodies, varying, according to the state of contraction in which they are found, from $\frac{1}{200}-\frac{1}{80}$th of an inch in their long diameter.

When fully extended, the *Echinococci* are divided by a constriction into two portions; an anterior somewhat conical part, and a posterior oval portion, notched at the extremity; attached to the posterior section, and, as it were, sunk in the notch, there is a small appendage of variable form, which usually appears to be clear and somewhat oval or pyriform, with an irregular ragged extremity.

The body of the *Echinococcus* consists of a very clear transparent substance, slightly granular or dotted internally, and limited externally by a well-marked structureless layer. Forming a circle round the conical anterior extremity there are from twenty to thirty strong hooks, which sometimes appeared to be in a single, sometimes in a double row. In the latter case the hooks of the upper row alternated with those of the lower. A delicate longitudinal striation, as if produced by muscular fibres, extends from the circlet of hooks through the anterior portion, becoming spread out and lost in the posterior.

The hooks (fig. 3) were about $\frac{1}{700}$th of an inch in diameter. Their outer half was formed by a strong, curved, conical claw, the inner half by a somewhat crooked process with a blunt end. From the posterior surface of the junction of these two portions a strong rounded spur passed backwards and gave the hook additional firmness in its place. The hook contained a cavity, a process of which passed into each of its portions. Altogether it was not unlike the thickened liber-cell of a plant.

Behind the circlet of hooks, the shape of a transverse section of the body is quadrilateral, and at each of the four corners a large rounded disc with a more or less flat surface is to be seen,—the sucker. In structure, when unaltered, the suckers appear to be homogeneous, with granules and two or three of the peculiar corpuscles to be described immediately, imbedded in their substance. Under the action of acetic acid, however, a radiated fibrillation frequently became visible.

Scattered through the substance of the *Echinococcus*, and giving it a very peculiar dotted appearance under a low power, a number of oval, strongly refracting corpuscles may be observed. They are very uniform in size, and have a long diameter of about $\frac{1}{250}$ th of an inch. They are what have been called the *calcareous corpuscles* of the *Echinococcus* ;—inasmuch, as in the *Cysticerci* and other cystic worms they have been observed to be converted into carbonate of lime ; but I believe that this is entirely a result of that peculiar degeneration to which the cystic Entozoa are so liable, and that, in the young and normal adult state, these peculiar corpuscles (which are found in all the *Cestoidea* and *Cystica*) are never calcareous, but are composed of an albuminous substance.

The mistake has arisen, I think, from two causes. In the first place, in old cystic worms these corpuscles are frequently converted into a calcareous substance, although they retain their transparency and strongly refracting powers ; and secondly, because when acid is added to a number of *Echinococci*, gas is very commonly developed from calcareous substances contained either in them or in the fluid in which they swim ; at the same time the action of the acid rapidly causes the corpuscles to become clear vesicles, so that nothing seems more natural than to connect the one circumstance with the other.

Having paid great attention to the process, however, I can, decidedly affirm—

1. That acetic acid dissolves out the contents of the corpuscles in young and fresh *Echinococci*, without the least evolution of gas from them ; and that the same assertion holds good of the corresponding corpuscles contained in the spirit specimens of *Tænia* and *Bothriocephalus* which I have examined.

2. That caustic ammonia produces little cavities and sometimes a concentric lamination in these bodies.

And, 3rdly, that in a spirit specimen of an *Echinococcus* from the Panther (which Dr. Hyde Salter kindly lent me), the corpuscles appeared vesicular without the action of any reagent.

It may be said then, that the peculiar strongly refracting cor-

puscles of the cestoid and cystic Entozoa usually contain an albuminous substance, and sometimes a fatty matter, but that this is very liable to become replaced by a calcareous substance.

Homologically, I think they are identical with the peculiar, elongated, strongly refracting, solid bodies, contained in the skin of both the *Dendrocœle* and *Rhabdocœle Turbellaria*, which in some marine *Planaria*-larvæ, according to Prof. Johannes Müller, are developed into true thread cells, similar to those of the hydroid Polypes. The thread cell of the latter is equally developed as a secondary deposit within a vesicle (nucleus ?) contained in the cells of the body ; the only difference would be, that whereas in the Polype the succeeding internal deposit takes place in the form of a spiral thread, in the cestoid or cystic Entozoon it takes place as a succession of simple layers, until the vesicle is full.

Aware of the discoveries that have been lately made by Siebold, Van Beneden and Guido Wagner, as to the extent to which the water vascular system is developed in the Cestoid Entozoa ; and unacquainted with what had been observed by Dr. Lebert[1] (vide *infra*), I particularly endeavoured to detect, in the quite fresh *Echinococci*, some evidence of its existence, and I was so far successful that I could very readily observe in several specimens (examined on the first day) a number of the peculiar flickering cilia so characteristic of this system of vessels wherever it exists. In spite of all my endeavours, however, I could trace nothing of the vessels themselves, in which, by analogy, one has every reason to believe the cilia are contained.[2] In one *Echinococcus* I observed six of these long flickering cilia in the positions indicated by the short wavy lines in fig. 1 (Pl. XXVIII. [Plate 21]). They were so distinct as to be perfectly measurable, their length being about $\frac{1}{3500}$th of an inch. They were excessively delicate, but broader at the fixed than at the free end, and they completely resembled the corresponding organs in the *Rotifera*,[3] *Naidæ*, &c.

Professor Owen has stated (article *Entozoa*, Todd's Cyclopædia, 1839) that the *Echinococci* (from the Pig) which he examined, moved "freely by means of superficial vibratile cilia," p. 118. There were certainly no such cilia upon the *Echinococci* of the Zebra.

[1] Prof. Virchow, and the colleagues before whom he laid his observations upon the occurrence of cilia in the pedicle of *Echinococcus* (vide *infra*), appear equally to have overlooked Dr. Lebert's excellent paper, although it is contained in Müller's Archiv for 1843.

[2] In the *Planaria torva* I have similarly observed the cilia but not the vessels.

[3] See the essay by the author on "*Lacinularia socialis*," &c. &c. in the Microscopical Journal, No. 1, 1852. (*Supra*, p. 126).

The movements of the *Echinococci*, so far as I witnessed them, were confined to slow, undulatory, peristaltic contractions. I found numbers in every stage of contraction, but I could not observe any actually performing the process. The head with the hooks, is drawn in first, as one meets with many forms in which the suckers only protrude at the extremity, like four knobs. The suckers then follow and are turned completely in, so that their proper outer surfaces look towards one another, the coronet of hooks lying beneath them. In this state, which has been so often described, the animal has not more than half its previous length, and takes on a great variety of forms, oval, rounded, heart-shaped, &c. Instances of these varieties are figured in both plates.

b. The secondary cysts.—When the fluid contained within one of the large *Echinococcus*-cysts is emptied into a glass vessel, it is at first turbid with minute white bodies, but these rapidly subside and form a white sediment at the bottom of the vessel. These white bodies vary in size from $\frac{1}{30}$th of an inch in diameter downwards to $\frac{1}{100}$th. They are the secondary cysts.

Under the microscope these bodies are seen to be delicate spheroidal sacs, containing *Echinococci*. The largest examined (Pl. XXIX. [Plate 22] fig. 9) had at least thirty of these in its interior. It consisted of a very transparent structureless membrane, apparently lined by a delicate granular film, which was most distinct near the pedicles of the contained *Echinococci*. These *Echinococci* in fact were not free like those contained in the primary cyst, which I have previously described, but each was attached by a delicate cord, more or less resembling the "appendage" of the free *Echinococcus*, to the inner wall of the secondary cyst (Pl. XXIX. [Plate 22] fig. 8), and radiated thence inwards. These *Echinococci* resembled in all respects those previously described, except that I could observe no ciliary motion in them[1]; they were in all conditions of protraction or retraction, and exhibited the ordinary movements. None were ever found free in a secondary cyst, and the members of each cyst, as well as those in different cysts, were as nearly as may be of the same size and degree of perfection.

The space left between them in the interior of the secondary cysts was sometimes filled with a clear fluid, and at others more or less obscured by granules. In none of those observed by me was there any trace of the peculiar mode of development of the contained *Echi-*

[1] This may well arise from my not having examined them till the 28th. Lebert appears to have found the observation of the cilia to be favoured by the interposed membrane of the secondary cyst (vide *infra*).

nococci from the granular contents of the secondary cysts described by Von Siebold (vide *infra*).

The membrane of these cysts was traversed by a meshwork of fine clear delicate vessels, with distinct walls and about $\frac{1}{10000}$th to $\frac{1}{16000}$th of an inch in diameter. These were not folds, as their lumen could be clearly seen at the edge of a cyst (fig. 8). They terminated in a somewhat wide space at the base of the pedicle of each contained *Echinococcus*, and in one instance I traced a vessel for some distance into this pedicle. There were no cilia nor granules contained in these vessels, but they precisely resemble those canals of which traces were seen in the Endocyst, and their development will, I think, show that they are identical with them.

I may anticipate so far as to say that I believe that these vessels represent the water vascular system of the parent-cyst.

A dark spot may be observed upon the surface of fig. 9. This was a blunt yellowish wrinkled process, like that represented in the lower portion of fig. 7. It was the only projection of the kind in this specimen.

When such a sac as this is burst the *Echinococci* become everted, and the secondary cyst turns itself inside out, so that the *Echinococci* appear to be seated like Polypes upon a central stem. This curious peculiarity has led to much misconception as to the mode of their attachment *within* the cyst. Von Siebold, however, pointed out the true nature of this process as far back as 1837[1] (vide *infra*).

The smallest free secondary cysts varied in size, as I have said, down to $\frac{1}{100}$th of an inch, when they contained only four *Echinococci*, (Pl. XXIX. [Plate 22] fig. 6.) These, however, were quite as large as those in the largest secondary cysts.

The structure of the middle-sized and small vesicles was in most respects the same as that of the large ones, but there was this difference, that they possessed, attached to their outer surface, by pedicles, a variable number of oval bodies of the same average size as the *Echinococci* or less, but presenting a yellow wrinkled appearance, containing very few corpuscles, often none, and either exhibiting no trace of the circlet of hooks (fig. 6) or offering only a few, dark irregular and withered looking ones (fig. 7). It was impossible to confound these *external* bodies with accidentally everted *internal* heads, three of which are represented at the upper part of fig. 7; the appear-

[1] The *Echinococci* are figured in this everted state by Chemnitz (quoted by Siebold, art. *Parasiten*, Wagner's Encyclopædia, &c.), by Erasmus Wilson (Medico-Chir. Transactions, 1845), and by Busk (Microscopical Transactions, 1846).

ance of the two being more markedly different than even the figure represents it.

I cannot help thinking that these withered *Echinococci*, for that, as will be seen presently, is what they really are, are what Mr. Erasmus Wilson has figured as developing forms (*loc. cit.*).

Development.—We have found free *Echinococci* and free secondary cysts contained in the fluid of the primary cyst: how do they come there? To answer this question we must return to the endocyst. I found adherent to, and growing from it, *a.* fixed *Echinococci*, and *b.* fixed secondary cysts.

a. Fixed Echinococci.—These, in various stages of development, are scattered all over the inner surface of the endocyst, as in the diagrams E. and F. (Pl. XXIX. [Plate 22]).

Elongated elevations of the endocyst (Pl. XXVIII. [Plate 21] fig. 5) are first seen: within these the circlet of hooks and then the corpuscles make their appearance: the elevation becomes a papilla, and the papilla, gradually constricting itself at the base, becomes the oval *Echinococcus*, attached by a narrow pedicle. In this state the slightest touch is sufficient to separate the pedicle from the endocyst, and then the *Echinococcus* is set free. The pedicle contracts upon itself so as to have a rounded form, but it very often betrays its previous adherence by the ragged fragments of the endocyst, which it carries with it.

Whether this is properly a normal process in the *Echinococcus* it is difficult to say, but as Dr. Guido Wagner and Van Beneden have shown, it occurs normally in the *Tetrarhynchidæ*, and it exactly resembles that detachment of the "tail" from the *Cercaria*, which takes place in the *Distomata*.

As little is it known whether the *Echinococci* undergo any further development. The suggestion first made by Delle Chiaje, that they may dilate into cysts and develope young *Echinococci* within themselves, appears to me highly improbable; and it is an hypothesis which is not needed to account for the secondary cysts.

b. Fixed Secondary Cysts.—The development of these indeed, takes place in such a manner as to preserve the homological relations of the *Echinococci* to the exterior of the parent. The secondary cysts, in fact, are thus formed: *Echinococci* are developed not only from the inner surface of the endocyst, but from its outer surface (Pl. XXVIII. [Plate 21] fig. 4). Their growth is probably accompanied by that of the endocyst itself, which thus becomes raised up from the ectocyst and projects into the general cavity (fig. 5). Of course any internal *Echinococci* which happen to be attached to this part of the endocyst are raised up with it (figs. 4, 5): they may be fewer or more according

to circumstances. The neck of attachment of the secondary cysts gradually narrows (fig. 4), and at last the secondary cyst, whose size depends entirely upon the number of *Echinococci* developed under the endocyst at one spot, is detached and falls into the cavity. So long as the secondary cyst remains attached, its external *Echinococci* have the normal clear appearance, and are in full health ; but when once it is separated, they appear rapidly to wither away and become yellow, losing their hooks and their corpuscles, and eventually disappearing. The original point of attachment of the sac remains as an obtuse cicatrice.

Von Siebold, who has beautifully described the development of the secondary cysts, has, I think (vide *infra*), mistaken the *one* mode of development of the *Echinococci* outside the endocyst for the *only* mode. He appears to have seen the endocyst, when he describes the "delicate membrane in which the young *Echinococcus*-heads are enclosed," and to *assume* merely, that this membrane bursts and sets the *Echinococcus* free upon the inner surface of the parent cyst. Understanding the mode of development to be as stated above, it is easy to comprehend how it is that the *Echinococci* are so nearly at the same stage of development in all the secondary cysts ; and that this stage has no relation to the size of the cysts. The existence of the external *Echinococci* upon the secondary vesicles in this way also, becomes not only intelligible, but almost necessary.

II. The theory which I have to offer of the nature of the *Echinococcus*, is based upon three facts which are now well established. 1st. That young Cestoid Worms, which, from some cause or other, have passed into any other part of the organism of the animal upon which they are parasitic, than the intestine, become abnormally dilated, at their posterior extremity ; and the anterior end may be retracted into the sac thus formed, which then invests it like a double serous sac—a structureless investment may be excreted round this encysted worm or it may not. Such an altered Cestoid Worm as this is called a *Cysticercus*.

2ndly. A dilated Cestoid worm, such as has been just described, may develope new "heads" with suckers and hooks all over its outer surface, never developing any upon its inner surface. Such a Cestoid worm is the *Cœnurus cerebralis*.

3rdly. The Cestoid worms all possess the power of gemmation (or it may be called fission) in their unaltered state: and Bendz (Isis, 1844) has distinctly shown that the vesicular extremity of the *Cysticercus* gemmates. Processes are formed and thrown off, and these develope appropriate heads and hooks, becoming complete *Cysticerci*.

Bearing these facts in mind, it is, I think, very easy to account for the *Echinococcus*-vesicles. The surfaces which produce the *Echinococci* must be *both external*; the *Echinococcus*-cyst therefore does not answer to the simple cyst of the *Cœnurus*, or of the protruded *Cysticercus;* but to the double cyst of the retracted *Cysticercus*, the upper half of whose proper outer surface forms the inner wall of the cyst in the retracted state (see Diag. D. Pl. XXIX. [Plate 22]).

Suppose the cyst, thus formed, to dilate and to develope a multitude of heads upon this upper half of the outer surface, after the analogy of *Cœnurus*: then the two walls being pressed together into one, it will appear like a simple cyst covered with heads internally (Diag. E.).

If, however, at the same time, in complete correspondence with *Cœnurus*, heads have been developed over the whole outer surface, we have the primary *Echinococcus endocyst* (Diag. F.).

Now the cyst may grow out at a particular point, and so form a bud which is cast off externally. This takes place in the *Echinococcus* of Oxen. But if it have surrounded itself with a dense cyst, analogous to that of the encysted *Tetrarhynchidæ*, such external budding cannot take place; and if the local growth takes place at all, it will produce a projection internally, and the internal fixed secondary cyst will be produced. These, narrowing at the neck and detaching themselves, become the free secondary cysts as was shown above.

The *Echinococcus* then is a species of *Tænia* which has become dilated and encysted; which has subsequently produced heads all over its external surface, and finally, budding, casts off its vesicular processes internally, because it has no exit for them externally.

Echinococcus is thus the most complex form of that change which young Cestoid Worms are liable to undergo if they wander from their proper nidus; the combination of hooks with suckers refers it to the genus *Tænia*, to which *Cœnurus* and *Cysticercus* may by similar reasoning be shown to belong; and, therefore, like these two latter genera, it must, as a genus, be abolished. It is probable however that *Cysticercus*, *Cœnurus* and *Echinococcus* are modifications of distinct species, or groups of species, of the genus *Tænia;* and are not mere varieties of one species produced by difference of locality. They are all three found in the brain, for instance.

As to the genus *Acephalocystis*, there is good reason for believing, that all genuine specimens of it are *Echinococcus*-cysts which have either not developed heads, or in which they have been overlooked.

The converse of the anatomical evidence as to the identity of

Echinococcus with a modified *Tænia*, has just been supplied by some very beautiful researches of Von Siebold's, published in the Annales des Sciences for 1852 (or Annals of Natural History, December, 1852). Von Siebold gave to young puppies spoonfuls of *Echinococcus*-cysts in milk. Upon opening them after a short time, he found *innumerable Tæniæ attached all over the surface of the intestine.* The cysts had been digested, but the living *Echinococci* had resisted the action of the stomach, and, freed from their imprisonment, had begun to develope joints. Growth had not gone on sufficiently to enable the learned Professor of Breslau to determine the species. He promises, however, a continuation of his researches; and it is to be hoped that we may soon have a complete clearing up of the difficulties with which helminthologists have so long been puzzled, from his able pen.[1]

III. The literature of *Echinococcus* exhibits a singular instance of the manner in which naturalists delay their own progress, by not attending to what has been done by their predecessors. Goeze wrote in 1782, and effectually demonstrated the cestoid relations of the *Echinococci*, as may be seen by the following extracts from his beautiful work (Versuch Einer Naturgeschichte der Eingeweidewürmer); nay, before his time, Pallas had on very good grounds conjectured the same thing, and yet half a century afterwards we find this all forgotten, and speculation rife as to the nature of the *Echinococci.*

Goeze thus describes the *Echinococcus*-vesicles (*op. c.* p. 258 *et seq.*):

"C. The small social granular Bladder tape-worm (Blasen-bandwurm: *Tænia visceralis socialis granulosa.*

"This is as it were an intermediate form between the great globular Bladder tape-worm .(*Cysticercus*), and the many-headed worm found in the brain of staggering Sheep.

"I had already read what Pallas supposes on this subject in the 'Neue Nordische Beyträge,' i. p. 85, when, by a lucky discovery, I made the whole matter out.

"Upon the 1st of Nov. 1781, I met with an excessively distorted Sheep's liver, which was so beset and penetrated by large and small watery vesicles,—the former as large as hens'-eggs, the latter as hazel-nuts,—that, externally, one could discern hardly anything of the substance of the liver.

"The animal itself was almost perfectly healthy. In its total size, this monstrous liver was about equal in breadth to the two hands;

[1] A full account of Siebold's investigations has, in fact, appeared in Siebold and Kölliker's 'Zeitschrift' for 1853, under the title "Ueber die Verwandlung der Echinococcus-brut in Tænien."—T. H. April, 1854.

and its length was about half an ell : the weight however was four pounds. I was obliged to divide it into two portions in order to be able to get it into a large jar (3 inches, glass) with spirit. When I pricked one of the vesicles with a needle, the water spurted out, as out of a fountain. I observed, however, that the distended vesicles contained nothing beyond a mere lymph and possessed no special internal vesicle. In separating the one portion of the liver I could not avoid damaging some of the vesicles contained in its interior. Out of these tolerably hard leathery external vesicles, fell bluish, callous (kallöse), internal vesicles, which were still closed. In their substance indeed they were somewhat softer than the outer vesicle ; but still far more cartilaginous than the vesicles of the globular, many-headed bladder-worms. On opening these there were found internally in different places a grayish granular matter like the smallest fish roe, which was united to a very delicate mucous membrane, [which] in water however immediately disappeared, so that the granules swam about by themselves. In a vesicle as large as a dove's egg there were thousands, so small that they could hardly be distinguished by the naked eye. Under No. 4. Tub. A of my microscope I could already perceive the organization of these corpuscles. Their form varied greatly ; sometimes heart-shaped with an indent above and a dark line ; sometimes pitcher-shaped, with two round knobs above, at each side one ; sometimes like a horse-shoe with a short dark middle line ; sometimes like a rounded handle, with an indent above and with two knobs laterally, and anteriorly rounded off with a dark circlet. When I used No. 1. Tub. A, I saw clearly that they were true tape-worms. The body flat with dark dots ; anteriorly four suckers, and on the obtusely rounded proboscis, the double circlet of excessively small hooks ; behind however, in each there was a small excavated indentation like an anus. The others were contracted in quite peculiar forms, and the dark median streak was the hook circlet. Under the compressor, the four suckers, the circlet of hooks and the points become much clearer. In these worms I have observed a circumstance which I have perceived in no other kind of bladder-worm ; namely that on pressure the delicate hooks are detached and float about freely.

"This kind of bladder-worm is distinguished then from that inhabiting the brain of staggering sheep by the following circumstances :—

"1. That the vesicles with the granular matter or with many thousand infinitely small worms, are covered by a strong leathery external vesicle in which they lie free.

"2. That their roe-like material swims about in the inner vesicle in a clear lymph, and the single worms are only united together by

a delicate mucous membrane, but are not as in those, essentially adherent to the bladder, and not even to their [own] membrane.

"3. That each of these granules or worms is several hundred times smaller than one of the white corpuscles or worms in the central bladder of the staggering sheep.

"This is then the same, but now explained phænomenon, which the acute Pallas has already observed; but has left without elucidation.

"In the 'Stralsund Magazine,' 1. St. p. 81, he has already directed the attention of observers to these points:

"'Whoso will consider the above description of the true bladder-worm will not perhaps with M. de Hæn deny to worms all participation in the origin of watery tumours and of Hydatids, at least it seems to me very probable that the unattached (unangewachsene) watery bladders seen by many observers in the human body—most frequently in abnormal cavities in the liver—are caused by a worm similar to, if not identical with, our bladder-worm, I say from a worm *probably resembling our* bladder-worm; for we find in the liver and lungs of Oxen and Sheep another wonderful kind of watery bladder, which seems to arise from nothing but some kind of animal germ; but however is widely different from our bladder-worm, and cannot have arisen from it.'"

Pallas, after describing some of the Hydatids, goes on to say:

"The water-bladder itself consists of a white, hardish, quite homogeneous membrane, which becomes thinner towards the caudal extremity; wherever it is lacerated it folds back, and may be best compared with a section (as thin as paper) of a boiled cartilage of a young animal. Within this external strong membrane is lined by a delicate structure or membrane, which is very easily separated from it, and is beset with a great number of small, white, commonly round, or oval, corpuscles. The corpuscles consist, as the microscope shows, of longish globules united together, whose substance appears to be dotted."

Subsequently (p. 261) Goeze quotes from the 'Nordische Beyträge,' 1. St. p. 83, thus:

"It is probable that the unattached hydatids which are at times observed in the human body (are), either of the same kind as the proper bladder tape-worm, or are the same as those singular watery bladders, which I have observed and described in the liver and lungs of diseased Calves and Sheep, and which are most certainly also to be ascribed to a living creature, and are not indistinctly organized (at least if we consider the inner membrane strewed over with granular globules).

"On reading through Leake's treatise upon the 'Staggers in the Sheep,' p. 85, it seems very probable to me that the bladders in the brain are more similar to those which I have described in the lung and liver in Sheep and Calves, than to the bladder worm which Tyson and Hartman have described before me (our globular one); nay, perhaps, that they even constitute one genus with the former. The small worm provided with a circlet of hooks and four suckers, in these vesicles—might be a development of the globules observed by me.

"I have at present no opportunity of examining these vesicles in the fresh state. Perhaps on applying a stronger magnifying power the granules might exhibit more organisation."

Consequently, Pallas did not at that time know what to make out of the granules of these vesicles. The peculiar organization of these he did not himself see, as I have now discovered, described and figured it. To whom then belongs the first and true discovery of the nature of the granules in the internal membranes of the singular Hydatids of the livers and lungs of Calves and Sheep?

But I wish that I could throw more light upon and explain the mode of origin of these vesicles, and upon the œconomy of the many thousand single worms socially united in a single bladder. Do they grow? do they disperse themselves? does each build its own dwelling? or where do they remain? shall our successors learn nothing on these matters?

Goeze's figures are very good.

The commonly received view of the relation between the cysts and their *Echinococci* appears to have been first advanced by Delle Chiaje in his *Elmintografia Umana*, p. 30.[1]

"The said worms, oval, narrowed at the two extremities and enlarged in the middle, are scattered irregularly over the interior of the vesicle. The extremity of the head is garnished with a crown of hooks deprived of suckers. In proportion as they enlarge, these little microscopical bodies take on, little by little, a spherical form, the hooks become detached, and new *Echinococci* are produced in such little bodies, which have transformed themselves into Hydatids. The new worms are the children (figliuolini) of the primitive Hydatid, which was a similar microscopic body. They have a proper vitality, different from that of the vesicle which contains them."

Müller, 'Jahresbericht,' 1836, describes the *Echinococcus*-cysts and their contents found in the urine of a young man labouring under renal disease.

[1] *Compendio di Elmintografia Umana.* Napoli, 1825. Compilato da Stephano Delle Chiaje.

The cysts had a laminated outer coat; some contained *Echinococci* and some none, but in other respects they were completely alike. The *Echinococci* exactly resembled the ordinary figures.

"In a few of the free ones, a trace of a membranous cord, looking as if it had been torn off, appeared at the posterior end of the body; as if the worms had at an earlier period been fixed."

Müller could not make out whether the *Echinococci* were fixed to the interior of the secondary vesicle or not.

Tschudi, 'Die Blasenwürmer, 1837,' observed the retrograding yellow *Echinococci*, which he assumes to be returning to the vesicular form. He considers that the "corpuscles" are ova, and that by their development in the interior of one of these retrograded *Echinococci*, the secondary cysts are formed.

Gluge, 'Annales des Sciences Naturelles, 1837,' describes the corpuscles of the *Echinococci* very carefully and minutely. He was the first to notice the peculiar structure of the endocyst. He says, "I have constantly seen in it a kind of arborization very similar to the formation in fibrinous exudations during the first stage of inflammation. We see these transparent bodies with slightly irregular contours resembling empty blood vessels and ramifying like them. I do not know whether these are true vessels, I merely draw attention to the fact."

In the same year (1837) the second edition of Burdach's 'Physiologie' appeared. It contains an admirable chapter by Von Siebold, upon the development of the Entozoa. Burdach's work is so little known, and so inaccessible in this country—that I think it worth while to subjoin the whole of what Von Siebold says upon this subject:—

"In the development of the *Echinococci* also, much has remained obscure. We must in them always distinguish two things; the parent vesicle, and the proper *Echinococci* enclosed within this. The maternal vesicle is covered internally by an excessively delicate epithelium, in which are contained corpuscles similar, though here generally elongated, to those which we have found in the neck of *Cœnurus*. In the fluid which the maternal vesicle encloses, we meet with a few *Echinococci*, which when they have everted their coronet of hooks and their suckers, allow nothing to be perceived in their interior but a few scattered glassy corpuscles. These *Echinococci* evidently arise from the inner surface of the parent vesicle. My own observations hereupon have been made upon *E. hominis*, *E. veterinorum*, and a new species which, since the number of its suckers varies very much, I will call *E. variabilis*. On examining the inner surface of the parent

vesicle we see little vesicles attached here and there, which contain a finely granular substance; out of this mass the *Echinococci* proceed (hervorkeimen), sometimes only one, sometimes two, six, seven, or more. A portion of the granular mass becomes, in fact, sharply marked off, forms a small roundish body, which, however, by one of its ends, still clearly passes into the rest of the substance; the rounded body gradually takes on a pea shape, the constricted portion elongates, and the body which has now assumed a more oval form, is connected only by a delicate viscid thread with the mass from which it sprang; we soon now observe in the interior of the body the circlet of hooks and the glassy corpuscles. The *Echinococcus*-head thus far developed now begins to move—everting and retracting its suckers and hooks; the whole body being at the same time sometimes elongated, sometimes contracted. The development of the *Echinococci* having proceeded to this stage, the delicate membrane in which they are enclosed bursts. The young *Echinococci* do not immediately fall out, for they are all connected to the inner surface of the membrane, which until now has enclosed them, by means of a delicate cord or process of the latter, which penetrates at the posterior extremity of the *Echinococcus*, through a pit, into the interior of the body of the *Echinococcus*. The pit looks almost like a sphincter, holding just that cord of the membrane; only after an interval do the cords and the bodies of the *Echinococci* become separated. The mode of connection of these cords with the bodies of the *Echinococci*, and their separation from them, reminds one completely of the relation which the bodies and tails of the *Cercariæ* have to one another. The membranous covering of the young *Echinococci* wrinkles up immediately when it is torn. The *Echinococci* become everted, and so form a rounded heap, in the middle of which the collapsed investment lies hidden, the *Echinococci* being attached to it like the polypes upon a polypidom.

"Such masses of *Echinococci* either remain for a long time hanging to the inner surface of the parent vesicle, or they become detached from it before the single *Echinococci* have separated from the wrinkled membrane. The granular mass contained in the vesicles is probably comparable with nothing else than with a yelk mass, which supplies the heads with the substance necessary for their development through those fine cords. For the rest, I will not undertake to decide whether all those larger and smaller vesicles, which contain *Echinococcus*-heads and float about free among fully-developed *Echinococcus*-heads in the cavity of the parent vesicle, are detached from the wall of the latter, or whether some few of them

do not arise from the free *Echinococcus*-heads themselves, which have developed *Echinococcus*-germs in their interior, and afterwards become distended into vesicles by them ; I was often surprised, in fact, to find upon free vesicles containing *Echinococcus*-heads, hooks attached, perhaps remnants of the destroyed circlet of hooks. In such vesicles of *E. variabilis*, in fact, I believe I could trace remains of the suckers. With greater difficulty can we understand the mode of origin and propagation of the maternal vesicle of the *Echinococci*. Since in *Echinococcus hominis* we often find smaller hydatids enclosed within larger ones, we must believe that the external hydatid is the parent in which the others have been subsequently produced. In what manner, however, this enclosure has taken place, I must leave as much unsolved as the origin of the parent vesicle itself."

The next step was made by Dr. Lebert, in his excellent paper (unfortunately without figures), "Einige Bemerkungen über Blasenwürmer," in Müller's Archiv for 1843. From this I make the following extracts :—

"In the most, even freshly examined hydatids, the animals no longer move. Yet not unfrequently, if many vesicles be examined living groups may be met with. The movement of the animal, while still in the maternal vesicle, consists partly in turning upon its axis, partly in a wavy contraction, comparable to a peristaltic movement. In the interior of these yet living and moving animals I have perceived ciliary motion very clearly. It appeared in the whole interior of the animal, and I could observe it for hours together. At first I could with difficulty distinguish the single vibrating cilia ; yet, partly after partial evaporation of the fluid in which the animals were contained, partly by modifying the light with a very fine perpendicular diaphragm, I could succeed in seeing the cilia themselves, which are slightly curved and somewhat hook-like, and hardly more than $\frac{1}{800}$ mm. in breadth. I have seen the single cilia with especial distinctness towards the margin of the animal ; commonly, however, they are indistinct, on account of the contemporaneous vibration of a certain number of cilia, which resemble in their motion a field of corn agitated by the wind. The observation of this ciliary motion was perhaps rendered more easy by the circumstance, that I observed the animals still adherent to the finely granular membrane which forms the parent vesicle, and which, in all probability, favourably modified the light."

"As to what concerns the development of the vesicles themselves, it seems to go on in the following manner :—upon the inner wall of

a cyst which contains *Echinococcus*-cysts, secondary cysts are formed, which, after they have attained a certain grade of development, become detached from the inner wall of the larger cyst, and fall freely into their cavities, but still show the remains of their attachment in a slightly pointed place: on the inner surface of these secondary vesicles tertiary ones are now formed in the same manner, and so on. The hydatid sacs then arise by a kind of endogenous formation similar to that which Prof. Müller has already so beautifully described in the development of a peculiar kind of hydatid tumours (Balggeschwülste ").

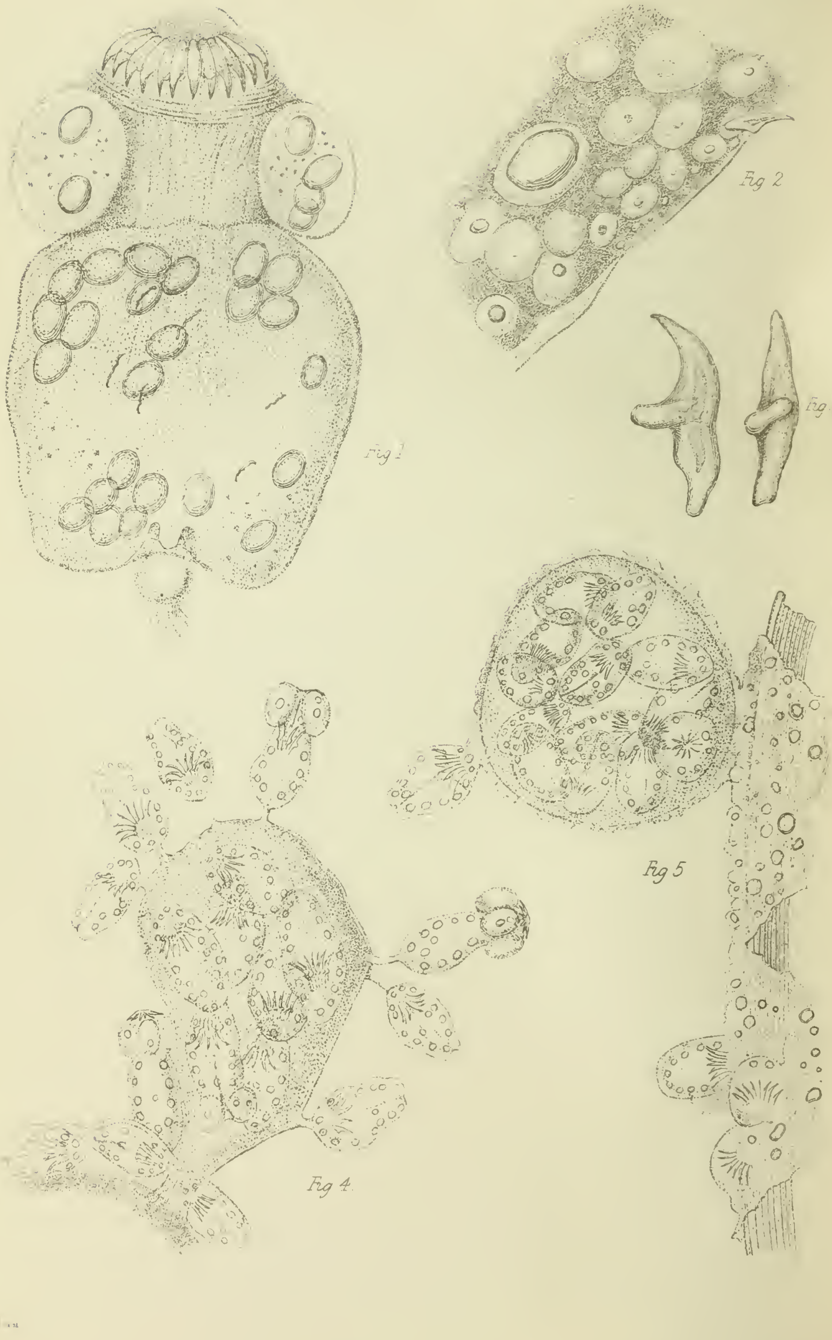
In his Article " Parasiten " (Wagner's Handwörterbuch d. Physiologie, bd. 2, 1844), Von Siebold, after recapitulating his view of the development of the *Echinococci* contained in Burdach's Physiologie, makes the following highly suggestive remarks :—

" Clearly as we can trace the development of the young of the *Echinococcus*, we understand very little of the mode in which the pill-box (eingeschächtelt) aggregations are produced. The multiplication of the vesicles certainly does not take place by division, nor by the formation of buds upon the outer surface of the parent cyst, as some have supposed. The hypothesis remains, that the young *Echinococci* cast off their circlet of hooks, become distended, lose their suckers, and so change into little *Echinococcus*-vesicles, in which a new brood then becomes developed. I must indeed confess that I have not directly observed this process. In any case, the young *Echinococcus* must be in a fit state to wander; and if it should be made out that new *Echinococcus*-vesicles proceed from them in the interior of the parent vesicles, we might also justly assume that the young *Echinococci*, wandering into other organs, or even into other persons, may thus lay the foundation for new colonies. Whether, again, there exists a special cestoid worm provided with sexual organs, with which the *Echinococcus*-vesicles stand in the same relation as the *Cercaria*-sacs do with certain *Trematoda*, time will show. If it be so the young *Echinococci* must change, having become separated from their pedicle, not into *Echinococcus*-vesicles, but by the elongation of the body into *Tæniæ*."

Finally, in the 'Verhandlungen der Physikalisch-Medicinischen Gesellschaft zu Würzburg' for 1850, (to which my attention was drawn by my friend Mr. Busk), I find the following notice:— " Herr Virchow described the ciliary movement which he had observed in the stem by which the young *Echinococci hominis* of Man are attached to the maternal vesicle,—a new observation for this genus."

[PLATE XXI]

Proc Z.S Annulosa Pl XXVIII



Development of Echinococcus

[PLATE XXII.]

Proc. Z.S. Annulosa Pl. XXIX.

Development of Echinococcus

I have here endeavoured to notice all those Memoirs which, at the time of their publication, made a definite addition to what was already known upon the structure of *Echinococcus*. The literature of the subject is somewhat voluminous, and hence the necessity of this limitation, and the consequent absence of any account of the valuable memoirs of Goodsir, Curling, Busk, and Erasmus Wilson, all of whom had been anticipated by the continental observers.

DESCRIPTION OF THE PLATES.

Pl. XXVIII. [Plate 21].

Fig. 1. A single detached Echinococcus-head, with the hooks and suckers protruded. The position of the six observed cilia is indicated by the wavy lines.

Fig. 2. A fragment of the Endocyst, with one of the abortive hooks.

Fig. 3. Fully formed hooks from an Echinococcus-head, seen in profile and in front.

Fig. 4. Secondary cyst still attached to the wall of the primary. The external Echinococci are seen in various stages of extension and contraction ; the internal Echinococci shine through the walls of the cyst.

Fig. 5. A similar cyst, with only one external Echinococcus. The relation of the Endocyst to the laminated Ectocyst is well seen, and the budding Echinococci on the inner surface of the former, which will eventually become external heads of secondary cysts.

Pl. XXIX. [Plate 22].

Fig. 6. A very small secondary cyst, with the remains of its pedicle above, and of an external Echinococcus below.

Fig. 7. Secondary cyst burst at the upper part and allowing three of the internal Echinococci to escape. The contrast of their appearance with the two dark and withered external Echinococci is well-marked.

Fig. 8. Portion of the wall of a secondary cyst, showing the ramified vessels, and the attachment of the internal Echinococci to its interior surface.

Fig. 9. A large secondary cyst with no external head, but with the remains of its pedicle appearing as a brownish spot.

Diagrams :—Hypothetical representations of—A. a young *Tænia ;* B. a *Cœnurus ;* C. a *Cysticercus ;* D. the same, encysted ; E. a *Cysticercus*, encysted, enlarged, and developing many heads (like *Cœnurus*) from the upper portion of its outer (now inner) surface ; E. a similar form, which developes heads from the lower portion of its outer (now wholly outer) surface, and so becomes an *Echinococcus*-cyst.

XX

ON THE IDENTITY OF STRUCTURE OF PLANTS AND ANIMALS

Abstract of a Friday Evening Discourse at the Royal Institution, April 15, 1853; *Royal Institution Proceedings, i.* 1851–4, *pp.* 298—302; *Edinburgh New Philosophical Journal, liii.* 1852, *pp.* 172—177

THE Lecturer commenced by referring to his endeavours last year to show that the distinction between living creatures and those which do not live, consists in the fact, that while the latter tend to remain as they are, unless the operation of some external cause effect a change in their condition, the former have no such inertia, but pass spontaneously through a definite succession of states—different in kind and order of succession for different species, but always identical in the members of the same species.

There is however another character of living bodies—*Organization;* which is usually supposed to be their most striking peculiarity, as contrasted with beings which do not live; and it was to the essential nature of organization that the Lecturer on the present occasion desired to direct attention.

An organized body does not necessarily possess organs in the physiological sense—parts, that is, which discharge some function necessary to the maintenance of the whole. Neither the germ nor the lowest animals and plants possess organs in this sense, and yet they are organized.

It is not mere external form, again, which constitutes organization. On the table there was a lead-tree (as it is called) which, a mere product of crystallization, possessed the complicated and graceful form of a delicate Fern. If a section were made of one of the leaflets of this tree, it would be found to possess a structure optically and chemically homogeneous throughout.

Make a section of any young portion of a true plant, and the

result will be very different. It will be found to be neither chemically nor optically homogeneous, but to be composed of small definite masses containing a large quantity of nitrogen, imbedded in a homogeneous matrix having a very different chemical composition; containing in fact abundance of a peculiar substance—*Cellulose.*

The nitrogenous bodies may be more or less solid or vesicular—and they may or may not be distinguished into a central mass (*nucleus* of Authors) and a peripheral portion (*Contents*, *Primordial utricle* of Authors)—on account of the confusion in the existing nomenclature, the Lecturer proposed the term *Endoplasts* for them.

The cellulose matrix, though at first unquestionably a homogeneous continuous substance, readily breaks up into definite portions surrounding each Endoplast;—and these portions have therefore conveniently, though, as the Lecturer considered, erroneously, been considered to be independent entities under the name of Cells:—these, by their union, and by the excretion of a hypothetical intercellular substance, being supposed to build up the matrix. On the other hand, the Lecturer endeavoured to show that the existence of separate cells is purely imaginary, and that the possibility of breaking up the tissue of a plant into such bodies, depends simply upon the mode in which certain chemical and physical differences have arisen in the primarily homogeneous matrix, to which, in contradistinction to the Endoplast, he proposed to give the name of *periplast* or *periplastic substance.*

In all young animal tissues the structure is essentially the same, consisting of a homogeneous periplastic substance with imbedded Endoplasts (*nuclei* of Authors); as the Lecturer illustrated by reference to diagrams of young Cartilage, Connective Tissue, Muscle, Epithelium, &c., &c.; and he therefore drew the conclusion that the common structural character of living bodies, as opposed to those which do not live, is the existence in the former of a local physico-chemical differentiation; while the latter are physically and chemically homogeneous throughout.

These facts, in their general outlines, have been well known since the promulgation, in 1838, of the celebrated Cell-theory of Schwann. Admitting to the fullest extent the service which this theory had done in Anatomy and Physiology, the Lecturer endeavoured to show that it was nevertheless infected by a fundamental error, which had introduced confusion into all later attempts to compare the vegetable with the animal tissues. This error arose from the circumstance that, when Schwann wrote, the primordial utricle in the vegetable-cell was unknown. Schwann, therefore, who started in his comparison of

Animal with Vegetable Tissues from the structure of Cartilage, supposed that the corpuscle of the cartilage cavity was homologous with the "nucleus" of the vegetable-cell, and that therefore all bodies in animal tissues, homologous with the cartilage corpuscles, were "nuclei." The latter conclusion is a necessary result of the premises, and therefore the Lecturer stated that he had carefully re-examined the structure of Cartilage, in order to determine which of its elements corresponded with the primordial utricle of the plant,—the important missing structure of which Schwann had given no account:—working subsequently from Cartilage to the different tissues, with which it may be traced into direct or indirect continuity, and thus ascertaining the same point for them.

The general result of these investigations may be thus expressed:—*In all the animal tissues the so-called nucleus* (Endoplast) *is the homologue of the primordial utricle* (*with nucleus and contents*) (Endoplast) *of the Plant, the other histological elements being invariably modifications of the periplastic substance.*

Upon this view we find that all the discrepancies which had appeared to exist between the Animal and Vegetable Structures disappear, and it becomes easy to trace the *absolute identity* of plan in the two,—the differences between them being produced merely by the nature and form of the deposits in, or modifications of, the periplastic substance.

Thus in the Plant, the Endoplast of the young tissue becomes a "primordial utricle," in which a central mass, the "nucleus," may or may not arise; persisting for a longer or for a shorter time, it may grow, divide, and subdivide, but it never (?) becomes metamorphosed into any kind of tissue.

The periplastic substance follows to some extent the changes of the endoplast, inasmuch as it generally, though not always, grows in when the latter has divided, so as to separate the two newly formed portions from one another; but it must be carefully borne in mind, though it is a point which has been greatly overlooked, that it undergoes its own peculiar metamorphoses quite independently of the endoplast.—This the Lecturer illustrated by the striking case of the Sphagnum leaf, in which the peculiarly thickened cells can be shown to acquire their thickening fibre *after the total disappearance of the primordial utricle*,—and he further quoted M. von Möhl's observations as to the early disappearance of the primordial utricle in woody cells in general,—in confirmation of the same views.

Now, these metamorphoses of the periplastic substance are two-fold: 1, Chemical; 2, Morphological.

The Chemical changes may consist in the conversion of the cellulose into xylogen, &c., &c., or in the deposit of salts, silica, &c., in the periplastic substance. Again, the periplastic substance around each endoplast may remain of one chemical composition, or it may be different in the outer part (so-called intercellular substance) from what it is in the inner (so-called cell-wall).

As to Morphological changes in the periplastic substance, they consist either in the development of cavities in its substance—*vacuolation* (development of so-called intercellular passages) or in *fibrillation* (spiral fibres, &c.).

It is precisely the same in the Animal.

The Endoplast may here become differentiated into a nucleus and a primordial utricle (as sometimes in Cartilage) or more usually it does not,—one or two small solid particles merely arising or existing from the first, as the so-called "*nucleoli;*"—it persists for a longer or shorter time; it divides and subdivides, but it never (except perhaps in the case of the spermatozoa and the thread-cells of Medusæ, &c.) becomes metamorphosed into any tissue.

The periplastic substance, on the other hand, undergoes quite independent modifications. By chemical change or deposit it acquires Horn, Collagen, Chondrin, Syntonin, Fats, Calcareous Salts, according as it becomes Epithelium, Connective Tissue, Cartilage, Muscle, Nerve or Bone, and in some cases the chemical change in the immediate neighbourhood of the endoplast is different from that which has taken place exteriorly,—so that the one portion becomes separable from the other by chemical or mechanical means;—whence, for instance, has arisen the assumption of distinct walls for the bone-lacunæ and cartilage cavities; of cell-contents and of intercellular substance as distinct histological elements.

The Morphological changes in the periplastic substance of the animal, again, are of the same nature as in the plant:—Vacuolation and Fibrillation (by which latter term is understood, not only the actual breaking up of a tissue in definite lines, but the tendency to do so)—*Vacuolation* of the periplastic substance is seen to its greatest extent in the "Areolar" connective tissue;—*Fibrillation* in tendons, fibro-cartilages and muscles.

In both Plants and Animals, then, there is one histological element, the Endoplast, which does nothing but grow and vegetatively repeat itself; the other element, the periplastic substance, being the subject of all the chemical and morphological metamorphoses, in consequence of which specific Tissues arise. The differences between the two kingdoms are, mainly: 1. That in the Plant the Endoplast

grows, and, as the primordial utricle, attains a large comparative size;—while in the Animal the Endoplast remains small, the principal bulk of its tissues being formed by the periplastic substance; and, 2; in the nature of the chemical changes which take place in the periplastic substance in each case. This distinction however does not always hold good, the Ascidians furnishing examples of animals whose periplastic substance contains cellulose.

"The Plant, then, is an Animal confined in a wooden case, and Nature, like Sycorax, holds thousands of 'delicate Ariels' imprisoned within every Oak. She is jealous of letting us know this, and among the higher and more conspicuous forms of Plants, reveals it only by such obscure manifestations as the shrinking of the Sensitive Plant, the sudden clasp of the Dionœa, or, still more slightly, by the phenomena of the Cyclosis. But among the immense variety of creatures which belong to the invisible world, she allows more liberty to her Dryads; and the Protococci, the Volvox, and indeed all the Algæ, are, during one period of their existence, as active as animals of a like grade in the scale. True they are doomed eventually to shut themselves up within their wooden cages and remain quiescent, but in this respect they are no worse off than the Polype, or the Oyster even."

In conclusion, the Lecturer stated his opinion that the Cell-theory of Schwann consists of two portions of very unequal value, the one anatomical, the other physiological. So far as it was based upon an ultimate analysis of living beings and was an exhaustive expression of their anatomy, so far will it take its place among the great advances in Science. But its value is purely anatomical, and the attempts which have been made by its author, and by others, to base upon it some explanation of the Physiological phenomena of living beings by the assumption of Cell-force, Metabolic-force, &c., &c., cannot be said to be much more philosophical than the old notions of "the actions of the vessels," of which physiologists have lately taken so much pains to rid themselves.

"The living body has often, and justly, been called, 'the House we live in;'—suppose that one, ignorant of the mode in which a house is built, were to pull it to pieces, and find it to be composed of bricks and mortar,—would it be very philosophical on his part to suppose that the house was built by *brick-force?* But this is just what has been done with the human body.—We have broken it up into 'cells,' and now we account for its genesis by cell-force."

XXI

OBSERVATIONS ON THE EXISTENCE OF CELLULOSE IN THE TUNIC OF ASCIDIANS

Quarterly Journal of Microscopical Science, i. 1853

A CAREFUL examination of a number of species of the Ascidian genera *Boltenia*, *Cynthia*, *Molgula*, *Phallusia*, *Syntethys*, *Aplidium*, *Pyrosoma*, and *Salpa*—including, therefore, every modification of the type, has led me to the following conclusions with regard to the structure of the mantle. The investigation was made with a full knowledge of what had been done by Löwig and Kölliker and by Schacht and I have only ventured to differ from them upon strong evidence.

1. In the most gelatinous forms of the test, as in *Syntethys* and *Salpa*, it consists of a soft homogeneous or delicately-striated basis, through which round nucleated cells (nuclei of Kölliker and Löwig) are scattered. These cells present no ramifications, and the presence of cellulose is demonstrated with very considerable difficulty. When the iodine solution is added, the whole mass becomes coloured yellowish-brown, the nucleated cells taking rather a deeper tint than the rest. The addition of sulphuric acid slightly contracts the whole substance, and if used with care, gives the edges the characteristic blue tinge. The cellulose is evidently diffused through the intercellular nitrogenous basis; for the first evidence of the operation of the sulphuric acid is seen in a slight diffused, even green shade, which is produced by the incipient blue reaction of the cellulose mingling with the existing yellow-brown colour. As the action of the test goes on, the edges of the membrane become deep blue, while the green tinge passes insensibly into the blue on the one side and into the yellow on the other.

As Schacht justly points out then, the substance of the test is not pure cellulose but cellulose deposited in a nitrogenous membrane. It

exists in the same condition as the calcareous salts in bone, or as the chondrin in cartilage.

Substituting cellulose for calcareous salts, the structure of the test of *Salpa* is exactly that of the bone of plagiostomous fishes (Leydig, Beiträge zur Anat. d. Rochen. Haie, 1852).

2. *Pyrosoma* has a firmer test, which contains far more cellulose. This is more readily detected by the iodine and sulphuric acid, but in its relation to a general nitrogenous basis precisely resembles that of *Salpa*.

The nucleated cells differ from those of Salpa in being thrown into very long processes which meet and unite—just like those of Volvox as described by Mr. Busk. On the other hand they assume exactly the appearance of bone corpuscles—though the processes are generally straighter and are rarely branched.

Making the same substitution as before, we have in the test of *Pyrosoma* a structure comparable to that of the lamina papyracea of the ethmoid bone.

3. In the *Phallusiæ* there is an indistinctly fibrillated basis, containing a large amount of cellulose in all essential respects resembling the foregoing. Nucleated cells, provided with irregular processes, are scattered through this substance.

The large cells described by Löwig and Kölliker and by Schacht are not cells at all, but are vacuolæ—very probably produced, like the cancelli of ordinary bone, by interstitial absorption. There is no lining membrane like that described by Schacht. With care the walls may be coloured deep blue to their very edges. The appearance of fibres is produced by the striation which runs through the whole mass, and is especially distinct upon the walls of the cavities. It exists after the action both of sulphuric acid and of caustic soda.

Lastly, the resemblance to perfect bone is completed by the canals which are hollowed out in the substance of the test for the vessels (or rather prolongations of the outer tunic, which is what they really are). In the walls of these canals I have frequently seen the nucleated cells projecting just as Kölliker describes them in the "medullary canals" or developing bone (Mikroskopische Anatomie, p. 369).

The spiral fibres described by Schacht are the muscular fibres surrounding the wider portions of the vessel-like prolongations.

Finally, with regard to the relations of the cells to the cellulose—anatomically and physiologically—I do not see any force in the distinction attempted to be established by Schacht between animals and plants. The nucleated cell of the Ascidian tunic answers exactly

to the primordial substance of the plant. The cellulose is deposited *outside* both. The amount of nitrogenous matter mixed up with the cellulose deposit appears to be a mere question of degree—and the nature and existence of an intercellular substance in the vegetable kingdom are still matters too much disputed to be good grounds of distinction.

The phsiological theory of Löwig and Kölliker, that the cellulose of the Ascidians is derived from the Diatomaceæ upon which they feed—is incompatible with the fact (Annals of Nat. Hist., Aug. 1852) that the larval Ascidian contains cellulose before any of its organs are developed.

To examine the test of an Ascidian for cellulose, I find the best way to be, to take a very thin section, and moisten it with a strong solution of iodine in iodide of potassium. After being thoroughly impregnated with the iodine, the superfluous fluid should be drained off, and the segment carefully *blotted* with the finger [or hair pencil]. A handkerchief or blotting-paper may readily give rise to error by leaving behind small fragments of vegetable fibre. A drop of sulphuric acid, as strong as can be procured, should now be added. If much cellulose is present, a deep-blue colour will appear immediately, beginning at the edges of the slice ; if there be but little, the colour will not appear for some time. The application of the test requires some care ; and while its success is most valuable evidence of the *presence* of cellulose, its failure is not by any means negatively conclusive, unless the experiment has been frequently and carefully repeated.

XXII

ON THE DEVELOPMENT OF THE TEETH, AND ON THE NATURE AND IMPORT OF NASMYTH'S "PERSISTENT CAPSULE"

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I AM desirous of setting forth in the course of the following pages, as concisely as may be, the principal results to which I have been lately led in the course of working over the development of the human and of some other teeth. I have directed my investigations, not to the general phenomena of dentition, our knowledge of the course of which, firmly established many years ago by Professor Goodsir, has not been affected, so far as I am aware, by any subsequent investigations, but to those points of structure and development upon which every writer, from the time of John Hunter to the present, seems to have formed, with more or less plausibility, an opinion of his own, different from that of all others.

I must suppose such a knowledge of the general course of development of the teeth as may be found in the ordinary hand-books of physiology—my limits allowing no unnecessary disquisition—and proceed at once to the questions whose discussion I am about to attempt. These are, firstly: What are the three structures which are concerned in the development of the teeth, viz., the pulp, the capsule, and the enamel organ, *morphologically*, or in relation to the parts of the mucous membrane from which they are developed?

Secondly: What is the relation of the dentine, the enamel, and the cement, to these organs?

Thirdly: What is the relation of the histological elements which enter into the composition of the soft parts, to the dentine, enamel, and cement, which are formed from, or within them.

These questions, I think, involve all the essential points connected

with the teeth. Having endeavoured to answer them, I shall inquire with what other organs of the animal the teeth correspond.

1. *The nature of the pulp, the capsule, and the enamel organ, with relation to the mucous membrane from which they are developed.*

The teeth are developed in two ways, which are, however, mere varieties of the same mode in the animal kingdom.[1] In the first, which may be typified by the Mackerel and the Frog, the pulp is never free, but from the first is included within the capsule, seeming to sink down as fast as it grows.

In the other the pulp projects freely at one period above the surface of the mucous membrane, becoming subsequently included within a capsule formed by the involution of the latter: a marked instance of this mode of development occurs in the human subject. The Skate offers a sort of intermediate stage.

If the thick and opaque, coloured, mucous membrane of the jaw of the Mackerel be torn away, and the alveolar edge of the jaw be then examined with a low power, minute germs will be seen to be imbedded in the substance of the jaw, among the large, fully-formed teeth. One of the smallest of those which I examined is figured at Pl. III. [XXIII.]. fig. 10. It was an oval mass, about 1-60th of an inch in long diameter; its upper part was roofed as it were by the epithelium of the gum; its sides were constituted by the continuation of the basement membrane of the mucous membrane of the mouth; within this was a homogeneous substance, containing numerous oval or rounded nuclei, about 1-5000th of an inch in diameter, and continuous with the lowest layer of the epithelium of the mouth. In the centre appeared a large conical mass, nearly as long as the sac, the proper tooth pulp. Pointed above, it widened below, and then gradually contracted again, so as to form an almost hemispherical lower extremity, which was united to the base of the sac by a narrow neck. In the upper part of the papilla the proper dental tissues had already begun to make their appearance; but below, a delicate membrane formed its outer boundary, and this passed directly into the basement membrane of the sac.

It is clear then, that in this case the papilla is wholly a process of the derm (or that which in a mucous membrane corresponds to it) outwards, while the sac is a process inwards of the same structure; and that the homogeneous substance, with its imbedded nuclei between the two, corresponds with the epidermis or epithelium.

[1] For the purposes of the present examination I have taken the Skate, the Mackerel, the Frog, the Calf, and Man, as accessible specimens of each of the great divisions of animals possessing teeth.

In the Frog the same relations essentially hold good ; the young teeth are here developed in minute sacs, which lie at the bottom of the dental groove in the upper jaw. I could never detect any free-projecting pulps (nothing, therefore, corresponding to the papillary stage in the human tooth), but the smallest and youngest rudiments of the teeth I found were oval or rounded sacs, 1-180th of an inch long, containing an oval papilla, about one-fourth shorter. Externally, these were bounded by a strong structureless basement membrane, which enclosed a homogeneous substance, containing nuclei in its cavities. These were rounded, and very close together, next to the basement membrane, but became transversely elongated in the inner layers and next to the pulp. This last was bounded by a structureless membrane, which at its narrow base became continuous with the basement membrane of the capsule.

In the Frog, then, the relations of the pulp and of the capsule are the same as in the Mackerel.

In the Skate, as is well known,[1] the young teeth are developed in longitudinal rows within a deep fold of the mucous membrane of the mouth, behind the jaw. So far as my examinations go, however, I find that this is not a mere simple fold, such as it has been described to be ; but its two walls behave just in the same manner as those of the primitive dental groove in man—that is, they become closely united in lines perpendicular to the direction of the jaw, so that partitions are formed between every two rows of teeth—transverse partitions again stretch between the separate teeth of each row, but these did not appear to me to be complete, terminating by an arcuated border below (*fig.* 11). Each longitudinal canal therefore answers to a single elongated mammalian follicle, or to that prolongation of the alveolar groove from which the posterior permanent molars are formed in man (*see* Goodsir), only the process does not go so far as in this case, the separate capsules remaining imperfect anteriorly and posteriorly. The lateral walls of the capsule, however, seem to me to have as much (or as little) " organic connexion with the pulp and attachment to its base " as in man, and the process seems to correspond with something more than the " first and transitory papillary stage of the development of the mammalian teeth." [2]

Each pulp is invested by a very distinct basement membrane whose continuity with that of the mucous membrane of the follicle is

[1] See Blake's ' Essay,' &c. 1801, in which the essential peculiarities of the development of the teeth in the shark and skate, and their mode of advance, are very well pointed out. He refers to Herissant and Spallanzani as having anticipated him.

[2] See Owen's ' Odontography,' p. 15.

very obvious. The epithelium of the follicle forms a thick layer, which sometimes, when the upper wall is stripped back, adheres to it—sometimes remains as a cap investing the papilla. Even when the latter does not take place, shreds of the epithelium frequently adhere to the papilla in the form of irregular, more or less cylindrical nucleated cells ; as often, however, the papilla, whether any of the proper tooth substances be formed or not, has nothing adherent to it, but presents a perfectly smooth sharp edge. Other portions of the epithelium, particularly towards the bottom of the follicles, are more or less altered and irregular, *frequently assuming the form of a stellate* tissue.

In the Skate, then, the follicle is an involution of the derm, the papilla is a process of it, and the epithelium between the two becomes metamorphosed sometimes into a peculiar stellate tissue. The same essential relations prevail as before.

In Man, some confusion has prevailed with regard to the homology of the various component parts of the tooth sac, though they might be readily enough deduced from the mode of development of the sac ; however, it is, I think, not at all difficult to obtain perfect demonstration upon this subject.

If a young tooth capsule be opened (say of a fœtus at the seventh month), whatever care may be exercised, it will always be found (Hunter, Bichât) that a space filled with a fluid exists between the inner surface of the capsule and the outer surface of the pulp—*the two are perfectly free from all adherence to one another*—the only substance between them, besides the fluid, being a more or less abundant whitish matter which sometimes adheres to the one and sometimes to the other (*see* Goodsir, *l. c.*).

If the tooth be very young, a structureless membrane, the m. preformativa of Raschkow (the basement membrane of Bowman), may be traced over the whole surface of the pulp, or if calcific deposition have already commenced, it may be found readily enough at any rate in the lower unossified part ; and it is not at all difficult to trace this in perfect continuity on the walls of the capsule—in fact into its basement membrane. The best way of seeing this is by detaching the whole sac from its alveolus, and then, laying it carefully open in a watch-glass, turn the capsule carefully back, transfer the whole to a glass plate, and cover it with a piece of thin glass. The continuity of the basement membrane of the pulp with that of the capsule is now evident enough under the microscope.

The wall of the capsule is often folded, and sometimes I have noticed villous processes, such as those described as vascular by Dr.

Sharpey.[1] Not unfrequently the basement membrane of the capsule is quite naked, but I have sometimes observed a lining of short cylindrical nucleated epithelium cells upon it.

I have said that a whitish substance lies between the basement membrane of the pulp and that of the capsule. It is delicate and friable, but frequently forms a more resisting layer towards the pulp. On this surface I have found it to be composed of a layer of elongated, more or less cylindrical epithelium cells 1-1000th of an inch in length, with or without nuclei, and adhering together in the direction of their short diameters. On the surface towards the capsule, on the other hand, this substance is composed of irregular cells united into a network (*fig.* 7), and very similar to those which have been described in the Skate. The structure of this substance, and its relation to the basement membrane of the pulp, and of the capsule, clearly indicate that it is nothing more than the altered epithelium of these organs.[2] It is the so-called "*enamel-organ*" of authors, and very wonderful figures and descriptions indeed have been given of it in various works upon the teeth. The only detailed,[3] and at the same time, as it seems to me, completely accurate account I have met with of this so-called enamel organ, is the very clear and admirable description by Mr Nasmyth, contained in his posthumous work, '*Researches on the Development, Structure, and Diseases of the Teeth*,' 1849. The merits of this gentleman have met with such scant justice that I cannot do better than let them speak for themselves in this place; those who work over the subject hereafter will not fail, I think, to acknowledge them as I have done.

Development of the Formative Organs of the Teeth, Follicular stage.—"At an early period of the follicular stage when the apex of the

[1] See also Goodsir, *l. c.* p. 17. In a child at birth "the interior of the sac had a villous, highly vascular appearance, like a portion of injected intestinal mucous membrane.' See also p. 25 of the same admirable essay.

[2] Goodsir ('Edin. Med. and Phys. Journal,' 1839) and Todd and Bowman ('Physiological Anatomy') state very distinctly that the pulp is an ordinary papilla, and the capsule an involution of the mucous membrane, and the latter justly described the membrana preformativa of the pulp as a basement membrane (p. 175), but they consider the "stellate tissue" and the enamel organ to be the "wall of the sac itself." Kölliker ('Mikr. Anat.,' p. 101) expresses the same opinion.

[3] Mr. Tomes ('Lectures,' &c., 1848) appears to me to have described the enamel organ very accurately, but he has, I think, failed to distinguish the proper enamel organ or epithelium of the sac from the submucous cellular tissue—the latter is his "reticular stage of the enamel pulp," the former his "second stage" or "stellate tissue," while what he calls the "transition part," p. 99, is, I think, the dense superficial layer of the capsule, very well described by Mr. Nasmyth (*vide infra*) as "the internal lamina of the dental capsule."

Professor Kölliker ('Mikr. Anat.,' p. 99 B) appears to me to have fallen into the same error.

papilla rises above the level of the surrounding fence of mucous membrane, a small quantity of whitish matter may be detected in the groove between the papilla and the follicle—this is the *enamel organ.* Not unfrequently the whitish matter has the appearance of granules which seem to have been separated from the surface of the follicle. These granular masses have a pearl white aspect, and are soft and friable. Under the microscope they are seen to be composed of cells which separate from one another upon the slightest compression. The cells offer considerable variety in respect of size and shape, some being small and round, others large and flattened, and furnished at one extremity with a delicate prolongation ; while others again are elongated and narrow, and have a defined and regular margin. They contain nuclei and nucleoli, and are covered on their interior by minute granules, which are also found in considerable abundance in their interstices."—p. 104.

" In the numerous examinations which I have made of the stages of growth of the teeth here described, the enamel organs did not appear to me to be attached either to the papilla or to the surface of the follicle. This may probably arise from the circumstance that all the embryos which I dissected had been kept for some time in diluted spirits of wine."—p. 105.

He then quotes Raschkow's account of the structure in the Lamb and Calf, and goes on to say,—

" In my own investigations made with the aid of one of the best microscopes of modern construction, and with a magnifying power of one-tenth of an inch focal distance, I found the enamel substance to be composed of cells of three different kinds.

" The first kind of cells are found in the interior of the organ, and compose its loose, soft, and easily compressible texture. They are flattened and triangular in form, and connected to adjacent cells by means of delicate filaments prolonged from one of their angles. These appendages have no analogy with the filaments of areolo-fibrous tissue, as declared by Raschkow. I have seen them in connexion with the cells of other tissues, and the error on the part of this observer must have arisen from the use of low microscopic powers.

" The second kind of cells are oval in shape, and form an envelope to the preceding : they are situated both upon the superficial and deep aspect of the latter.

" The third kind of cells occupy the deep stratum of the enamel organ, lying in contact with the dental papilla. They are narrow and oblong in shape, and are arranged closely side by side ; one of their extremities being in relation with the papilla, the other being directed

outwards. They are firmly connected together, and have a radiated position in respect of the papilla. It is to the layer formed by these cells that Raschkow has assigned the name of enamel membrane. Taking this view of the construction of the enamel organ, I cannot perceive any grounds for the division of it into two parts suggested by the description of Raschkow. It is obviously nothing more than a single organ, and the difference in the form and arrangement of the cells must simply be regarded as a transition of the first and second kinds into those of the third—the latter being in the state of preparation for the reception of the calcareous salts.

"The mucous membrane which rises in the form of a ring fence around the papilla developed from the dental groove is the future *dental capsule*. At an early period it is difficult to determine to what extent the internal surface of the growing follicle differs from mucous membrane. That it does so may be inferred from the change in function which it assumes; and at a later period, when the follicle is about to close, the difference in its organic character becomes strikingly obvious. For example, it is white, silvery, loose, and rugous, and easily falls into folds, and, under the microscope, offers the appearance of a number of minute cells possessing characters widely different from those of the epithelium.

"A portion of the internal lamina of the dental capsule, placed under the microscope, shows it to be composed of layers of cells loosely arranged, and separated by interspaces equal to half the diameter of the cell. The cells are oval in shape, and provided with one or more distinct nuclei, and they contain in their interior a small quantity of granular matter. The internal lamina of the dental capsule maintains but a slight degree of adhesion with the enamel organ, and possesses no vessels. Subjacent to it is a network of blood-vessels, supported by a web of areolo-fibrous tissue formed by the interlacement of fine homogeneous filaments, among which nucleated cells are not unfrequently observed."—p. 107.

Saccular Stages.—When the sac closes—

"The space between the pulp and the sac becomes filled with a fluid secretion which distends its cavity, and often produces a conspicuous enlargement in the situation of the tooth."—p. 108.

"On the part of the capsule corresponding with the sides and neck of the crown is a flat portion of the enamel organ, which is destined to the formation of the enamel in that situation. This lamina has a well defined inferior border at a later period in the growth of the enamel organ; the appearance which it presented of a gelatinous mass is lost, and the substance contracts into a membranous layer. At this

time also the prominences from the internal surface of the capsule have enlarged, and have become vascular and more closely adherent to the enamel organ. Some writers have inferred from this appearance that the enamel organ itself becomes vascular,[1] but this is not the fact; it is simply that portion of the capsule which lies in contact with the enamel organ that presents the vascularity referred to.

"The dental capsule being originally, as we have seen, a production of the mucous membrane of the alveolar groove, is attached by its external surface to the neighbouring soft parts by means of loose areolo-fibrous tissue. Blood-vessels ramify very freely in this tunic, and from the interlacement which they then form, numerous capillary loops are given off, which extend into the superficial portion of the membrane. These vascular loops are separated from the enamel organ by a delicate layer of cells, the characters of which have been already explained.

"Not the least interesting of the features attendant upon the development of the teeth is the relation which the capsule bears to the pulp and to the tooth at various periods of its growth. In the follicular and early periods of the saccular stage, previously to the commencement of the formation of the ivory, the capsule is continuous with the base of the dental papilla;[2] and at a subsequent period, when the ivory of the crown forms a complete covering to the pulp, the same arrangement takes place. But at a more advanced stage in the growth of the tooth, when its formation has proceeded beyond the limit of the crown, the capsule attaches itself closely around the neck, and the connexion of the two structures is so firm, that every attempt to effect their separation generally results in the laceration of the membrane. The continued growth of the tooth carries the capsule upwards with the rising alveolus to the under part of the gum, which now stretches over it; when pressed upon by the surface of the crown, it becomes atrophied and absorbed. No portion of the capsule seems to pass down into the alveolus."—p. 110.

Everything that I have seen confirms this admirable description as to matters of fact, and the only objections I shall have to offer are to certain of Mr. Nasmyth's conclusions.

In Man, then, as in the Skate, the Mackerel, and the Frog, the

[1] Raschkow, in a note appended to his Researches, remarks that he has observed the enamel organ to receive blood-vessels in certain parts, and believes the parenchyma of the organ to be pervaded by capillary vessels. The conclusion which he deduces from this observation is, that the enamel organ was from the beginning joined to the capsule.

[2] It passes upwards over it, forming a distinct envelope, separated from the layer of mucous membrane externally.

tooth-pulp is a dermic process bounded by its basement membrane; the capsule is an involution of the derm, bounded by its basement membrane; and the epithelium of these organs lies between them, having in this case received the name of "*Enamel-organ*," from the supposition that the enamel was developed by the calcification of its elements. Of this, however, I shall speak below.

There is an important difference between the dental sac of the Calf and that of Man, which has given rise to much confusion.

The "actinenchymatous" tissue (Raschkow) of the former does not at all correspond with the stellate tissue of the latter, as has been assumed by all writers. In fact, in the Calf the wall of the capsule is separated by only a very narrow space from the surface of the pulp, and this space is completely filled up by elongated cylindrical epithelium cells, which glue the capsule to the pulp. Between the basement membrane of the capsule and the alveolar wall, indeed, there is a very wide interval (see Owen, *l. c.*, pl. CXXII. *a*, fig. 9 *e*) occupied by Raschkow's actinenchyma. This, however, is nothing more than a loose submucous cellular tissue of the gum, similar to that so well described by Mr. Nasmyth in the wall of the capsule of man. Professor Owen says (*l. c.*, Introduction, p. lix.) that "no capillaries pass from the capsule into the actinenchymatous pulp of the enamel. But those which I have examined do not bear out this statement; in fact, this tissue presents one of the most beautiful and obvious vascular networks with which I am acquainted.[1]

The true homologue of the "enamel organ" in Man therefore, in the Calf, is not the actinenchymatous tissue, but the thin layer of epithelium between this and the pulp. The general relations of the different dental organs are in other respects, the same in the Calf as in Man.

I may now proceed to the second question. *What is the relation of the proper dental tissues to the three organs of the tooth capsule?*

The answer is shortly this. Neither the capsule nor the "Enamel-organ" take any direct share in the development of the dental tissues all three of which—viz., enamel, dentine, and cement—are formed beneath the membrana preformativa, or basement membrane of the pulp. In proof of this assertion, I have to offer the following facts:— If, in the human fœtus of the seventh month, a dental capsule (say of an incisor) be treated as I have above described, it will generally happen that the surface of the young tooth-cap appears quite smooth under a low power; or it may be that a few of the elongated cells of

[1] Blake, who wrote in 1801, mentions the vascularity of the "spongy" outer membrane of the tooth sac in the calf; he says it is "very vascular."—p. 81.

the "*organon adamantinæ*" adheres to it. In any case the adhesion is loose, and these cells may be readily detached. Under a higher power the surface of the upper part of the ossified cap appears reticulated, the meshes being about 1-5000th of an inch in diameter. At the lower part, where only a thin layer of dentine is formed, this appearance is less distinct, but the surface is somewhat wrinkled the wrinkles sometimes forming large and pretty regular meshes. Viewed in profile, these wrinkles are seen to be produced by the folding of a delicate structureless membrane, which is continuous below with the *membrana preformativa.* Towards the apex the tooth substance is almost too opaque to make much out of it; the yellowish enamel, however, can generally be distinguished from the dentine.

Now, while the object is under a low power of the microscope, add some strong acetic acid; a voluminous transparent membrane will immediately be raised up in large folds from the whole surface of the tooth. If the acetic acid be pretty strong, it soon softens the substance of the tooth a little, and then a slight pressure exhibits very distinctly the *ends of the enamel fibres under this membrane.* There can be no question about this fact, as I have been able to demonstrate it to the satisfaction of my friends, Mr. Busk and Professor Quekett. The membrane is about 1-2500th to 1-1600th of an inch thick, perfectly clear and transparent, and under a high power exhibits innumerable little ridges upon its outer surface, which bound spaces sometimes oval and sometimes quadrangular, and about 1-5000th of an inch in diameter. Furthermore, at its lower edge this membrane gradually loses all structure, and passes into the *membrana preformativa.*[1] *In fact, it is the altered membrana preformativa itself*, no trace of which has ever yet been found in the locality in which, according to the prevalent hypotheses upon the development of the teeth, it should exist—viz., between the enamel and the dentine.

In the Calf[2] a similar membrane may be demonstrated, but it is much more delicate, and I have not seen the peculiar areolæ upon its surface.

In the Frog, in which the layer of enamel is very thin and structureless, the membrane (*fig.* 8) may be very readily demonstrated by the action of dilute hydrochloric acid, which in this animal, as in the Mackerel and Skate, dissolves out the enamel layer at once, while it only acts gradually upon the dentine.

[1] It is stated, by all the writers on the subject whom I have consulted, that the membrana preformativa is the first portion of the tooth which ossifies. This statement, however, is never supported by evidence; and my own observations lead to precisely the reverse conclusions.

[2] *See* Hassall, Micr. Anatomy, p. 318.

In all these animals I have examined the smallest teeth I could find perfectly entire, without any rough mechanical treatment, which I should think would destroy the delicate membrane.

In the Frog, its surface is in parts *reticulated, as in Man;* in the Mackerel and Skate (*figs.* 9, 12) I have been unable to find any such reticulation. In both these the enamel forms a conical cap of almost structureless or obscurely fibrous substance at the extremity of the tooth, while the layer upon the body of the tooth is very thin.[1] In the Skate it is thick, dense, yellowish, structureless, and perfectly smooth; but in the Mackerel it is developed upon the lateral edges of the young tooth into sharp notched processes; lines stretch across the body of the tooth from these, not unlike the contour lines one sees on the enamel of a young human tooth.

A membrane, corresponding with that which has been described in the human subject then, is also found in members of each of the other groups of Vertebrata which possess teeth. In the human subject, and in Mammals, this membrane was discovered, and very accurately figured and described, fourteen years ago (that is, in January, 1839, in the 'Medico-Chirurgical Transactions), by Mr. Nasmyth, under the name of the "persistent capsular investment." No question has ever been raised as to the right of Mr. Nasmyth to this discovery; but it is remarkable, that neither in Professor Owen's 'Odontography,' which is the first subsequent work upon the teeth, nor in Professor Kölliker's 'Mikroskopische Anatomie,' which is the last, is there any notice of Mr. Nasmyth's discovery. Kölliker, indeed (*l. c.*, pp. 76, 77), describes the structure as "schmelz-oberhäutchen," but his description is not so good as that of Nasmyth, and he states that it does not extend over the cement—Nasmyth having shown that it does. Unfortunately, however, the latter, like all who have succeeded him, misled by the supposed mode of development of the enamel from the enamel-organ, imagined that as the "persistent capsule" was outside the enamel it could be nothing else than the membrane of the dental capsule; and hence the erroneous description of the adherence of the latter to the crown of the tooth, which I have already quoted. Had he chanced to examine a tooth before its eruption, he would at once have seen the incorrectness of his hypothesis.

[1] As this "dense exterior layer" may be dissolved out by dilute acid, leaving the "membrana propria of the pulp," which is very much thinner, standing, it is quite clear that it is not "formed by the calcification of the membrana propria of the pulp, which therefore precedes the formation of ordinary dentine."—(*Odontography*, p. 17). Why should it not be called enamel? It has at least as much claim to this title as that of the Frog.

Since then this "Nasmyth's membrane" is identical, on the one hand, with the persistent capsule which lies external to both enamel and cement, and, upon the other hand, with the preformative membrane of Raschkow, or otherwise with the basement membrane of the pulp; it is clear that all the tissues of the tooth are formed *beneath the basement membrane of the pulp;* in other words, they are all true dermic structures—none epidermic.[1]

The third problem was, the relation of the histological elements of the soft parts (that is, as we now see, of the pulp) to the Dentine, Enamel, and Cement.

Three theories have been prevalent as to the mode of development of the dentine. The first, the old *excretion theory*, need not be considered here, as it has been given up on all sides. The second, the Conversion theory, consists essentially in the supposition that the dentine is the "ossified pulp;" that the histological elements of the pulp become calcified and converted directly into the dentine—the arrangement of the elements of the dentine depending upon that of the elements of the pulp. This is the doctrine maintained by Blake, Schwann, Nasmyth, Owen, Tomes, Henle, Todd and Bowman, and, more or less doubtfully, by Kölliker and Hildebrandt.[2] The third theory is that contained in the remarkable phrase of Raschkow.

"Postquam . . . fibrarum dentalium stratum depositum est (quoted by Schwann) idem processus continuo ab externa regione internam versus progreditur *germinis dentalis parenchymate materiam suppeditante* . . . Conversæ fibrarum dentalium flexuræ quæ juxta latitudinis dimensionem crescunt, dum ab externa regione internam versus procedunt sibi invicem appositæ continuos canaliculos effingunt, qui ad substantiæ dentalis peripheriam exorsi multis parvis anfractibus ad pulpam dentalem cavumque ipsius tendunt, ibique aperti finiuntur novis ibi quamdiu substantiæ dentalis formatio durat fibris dentalibus aggregandis inservientes."

[1] That the enamel is not formed directly from the enamel pulp might have been concluded from Professor Goodsir's observations (*l. c.*, p. 25). He says, "The *absorption* (in the granular matter) goes on increasing as the tooth substance is deposited, and when the latter reaches the base of the pulp, the former disappears, and the interior of the dental sac assumes the villous vascular appearance of a mucous membrane. This change is nearly completed about the seventh or eighth month." It will not be said, however, that the growth of the enamel ceases at the seventh or eighth month.

[2] Dr. Sharpey, on the other hand, with characteristic caution, after citing the statements of some of the advocates of the Conversion Theory, adds, "We must confess that, after a careful examination of the human teeth, we have been unable to discover any of the above-mentioned changes, except the enlargement of the more superficial cells of the pulp, and their elongations in the immediate vicinity of the dentine."—Quain and Sharpey, p. 988.

The dentinal substance, that is, is deposited within the pulp beneath the membrana preformativa in definite masses (Raschkow calls them fibres, to which, indeed, under a low power they have a remarkable resemblance), the gaps between which eventually constitute the dentinal tubules. This, if a name be wanted, might be called the Deposition Theory, and is especially characterized by its asserting that the histological elements of the pulp do not enter *as such* into the dentine. The following description of the young dentine in the human subject holds good for all the animals which I have examined; and if it be true, I think the incorrectness of the Conversion Theory necessarily follows.

To justify my own method of procedure, however, I am necessitated to remark that I have been unable to verify the statement of Professor Owen (*l. c.*, Introduction, p. xxxix.), that the teeth of Man "will not yield a view of the cap of new-formed ivory and the subjacent pulp in undisturbed connexion by transmitted light with the requisite magnifying power." On the contrary, I have found it sufficiently easy, by cutting off the half-ossified cusp of a young molar, or even by submitting an entire canine or incisor to slight pressure, to obtain a most distinct view of the pulp in undisturbed connexion with the dentine, and in a profile view. Indeed, had other observers adopted this method, I do not think they would have been led to consider the lacunæ in young dentine, whose true nature was demonstrated by Raschkow, as metamorphosed nuclei of the pulp.

When the ossifying boundary of a tooth-pulp is examined in the way which I have here pointed out, it is seen that where dentification has not begun, the membrana preformativa is in immediate contact with the substance of the pulp, composed of a homogeneous transparent base, in which closely-arranged "nuclei" are embedded. These are rounded or polygonal, apparently vascular; contain one or more granules, and are about 1-2500th—1-3500th of an inch in diameter. Passing towards the ossifying edge, we see in the profile view a clear, more strongly refracting layer, gradually increasing in thickness, which begins to separate the proper substance of the pulp from the membrana preformativa. This is at first quite structureless to all appearance, both in this view and in one perpendicular to its surface. When it has attained a thickness of 1-2500th of an inch, however, it acquires a sort of mottled appearance in the profile view, while superficially numerous very minute irregular cavities, about 1-5000th of an inch apart, present themselves (fig. 5). In a thick portion of the dentine (3-5000ths) these cavities are very readily seen in the profile view to be elongated into canals; superficially they are rather larger;

and as they run somewhat obliquely it may very readily happen that, unless the focusing of the microscope be very careful, one will run into the other, and so produce the appearance of fibres described by Raschkow.

This young dentine is as transparent as glass. No trace of "nuclei" can at any time be discovered in it; the bodies which have been described as such being, as I have said, simply lacunæ; nor, if strong acids be used so as to dissolve out the calcareous matter, are any nuclei brought to light, though those which exist in the pulp became much more distinct, and even coarse, in their outlines. Again, if to a pulp thus treated, a weak solution of iodine be added, the nitrogenous substance of the pulp is immediately coloured deep yellow, the nuclei themselves becoming brown; but the dentine remains pale except that here and there a yellow process of the matrix of the pulp may be seen stretching a little way into one of the canals of the dentine. I have only observed this, however, once. I believe that these facts afford sufficient demonstration that the pulp is *not* converted directly into the dentine, and that the structure of the latter does not depend upon the calcification of pre-existing elements.

I am the more satisfied with this negative evidence, as in young bone it is easy to demonstrate the "nuclei" in the lacunæ by the aid of acids, &c.

As to whether the perpendicularly crowded "nuclei" of the pulp under the dentine disappear, or whether they are merely pressed inwards, I cannot pretend to offer a decisive opinion. The former supposition, however, if we may judge by the analogy of bone, appears more probable. Dentine, in fact, might be considered as a kind of bone, in which the lacunæ are not formed in consequence of the early disappearance of the nuclei, whose persistence for a longer or shorter period appears to be the sole cause of their existence in bone.[1]

Still less can the enamel be produced by any *conversion* of a cellular structure. Between it and anything which can be called a nucleated cell it has on the outer side Nasmyth's membrane; on the inner, the layer of dentine, which in Man is formed before it. The fibres of which it is composed are structureless, and almost horny;

[1] I have here no space to enter into the discussion of the various hypotheses and assertions, respecting the development of the dentine, made by the various authors whose names I have cited. I trust it will not on that account be supposed that I have neglected to make myself acquainted with them. But there are two statements to which I must refer in confirmation of my own view. The one is that by Dr. Sharpey already quoted: the other is the very just declaration (in italics) by Professor Kölliker (Handbuch, p. 386), that "*the most careful investigation exhibits no trace of any elongation of nuclei*" in the peripheral cells of the pulp.

and I think we must be content for the present to consider its existence and its structure as ultimate facts, not explicable by the Cell Theory. It is particularly worthy of notice that in the Skate the dermal teeth or plates on the upper surface of the head have as distinct a layer of enamel as those of the mouth, though in this case there is most assuredly neither rudimentary capsule nor "enamel organ."

In a morphological point of view, the relations of the cement show it to be homologous with the enamel. In a very beautiful section of a human tooth from Mr. Busk's cabinet, the upper portion of the cement exhibits in places a very distinct transverse striation, resembling its perfect enamel. But the transition of the one structure into the other is best exhibited in the young Calf by the cement of the fang of a molar which had not cut the gum. Here it is a white substance, from which generally a fitting section can be cut only with some difficulty, in consequence of its friability. The layer is about 1-40th of an inch thick, and consists of an external delicate structureless Nasmyth's membrane; internal to which three-fourths of the thickness of the layer are formed by parallel fibres 1-5000th of an inch in diameter, quite structureless, and completely resembling enamel fibres, but absolutely enormous (as much as 1-60th of an inch) in length. These fibres were softened and rendered pale by the action of caustic ammonia. The inner fourth of the layer of cement was composed of an inextricably interlaced body of such fibres, united into a mass, which in some places was almost homogeneous, by calcareous salts, and containing here and there lacunæ 1-1600th of an inch in length, similar to those of bone. That this structure was the young cement is certain, inasmuch as no enamel is formed on the fang of the tooth, to say nothing of the presence of the lacunæ. On the root of the fang of the molar in front of this, which had cut the gum some time, and had come into use, the cement had the ordinary structure. It may be worth while to add that in these teeth the capsule, though closely connected with the outer surface of the fang, could be readily stripped from it, and then exhibited a layer of epithelium upon its inner surface, showing clearly that the cement was not derived from its ossification.

It may be concluded, then,—

1. The teeth are true dermic structures, formed by the deposit of calcareous matter beneath the basement membrane of a dermic papilla, or that which corresponds with one.

2. Neither the capsule nor the "enamel-organ," which consists of the epithelium of both the papilla and the capsule, contribute *directly*

in any way to the development of the dental tissues, though they may *indirectly*.

3. The histological elements of the pulp take no direct part (except, perhaps, eventually in the cement) in the development of the dental tissues, becoming either absorbed or being pressed in by the gradual increase of the latter. The Conversion Theory is, therefore, as incorrect as the Excretion Theory, and the dentine is formed, not by ossification of the histological elements of the pulp, but by deposition in it, " parenchymate materiam suppeditante."

I have already exceeded my limits, and I must, therefore, dismiss my last point very concisely. The true homologues of the teeth in Man are, I think, the Hairs. As Hildebrandt says, " As the Hairs in their bulb (sac), so the Teeth are developed in their capsules." The stage of the free papilla, which does not occur in the hairs of man, is absent in the teeth of the Mackerel and Frog, and, indeed, it would seem in the permanent dental capsules of man also.

Substitute corneous matter for calcareous, and the Tooth would be a Hair. The cortical substance of the hair contains canals not unlike those of the dentine; its relation to a dermal papilla is the same as that of the dentine :[1] for although it is universally stated to be such, I think it can be shown that the hair shaft is *not* an epidermic structure, but a dermic one.

Again, the so-called cuticle of the hair corresponds in all respects, except absolute and relative size, with the enamel—its inner layer with the enamel proper—its outer with Nasmyth's membrane. On the root of the hair the cuticle is not continuous with the proper epidermic cells, but with a structureless membrane, which occupies more or less distinctly the place of a *membrana preformativa*. The two root-sheaths, again—true epidermic structures, but which do not enter all into the construction of the hair proper—represent the altered and unaltered portions of the "*enamel-organ*."

Hairs and *Teeth*, then, are organs in all respects homologous, and true dermal organs. Under the same category, probably, will come Feathers and the Scales of fishes.

The Nails, on the other hand, seem to be purely epidermic, at least according to Kölliker's account of their development (*l. c.*, p. 119); and in that case they are the homologues of the root-sheaths and enamel-organs of Hairs and Teeth.

[1] *See* Todd and Bowman, p. 175.

DESCRIPTION OF PLATE III [XXIII.].

The letters refer throughout to the same or corresponding parts.

a. The Mucous Membrane of the mouth.

b. The Lip.

c. The Alveolus.

d. The Pulp.

e. The Dentine.

f. The Enamel.

g. The Basement Membrane of the Pulp.

g.[1] Nasmyth's Membrane especially.

h. The "Enamel-organ" or Epithelium of the Capsule.

i. The Basement Membrane of the Capsule, with its subjacent condensed tunic. Hunter's inner, vascular, capsule.

k. The loose submucous cellular Tunic. Hunter's outer, non-vascular, capsule.

Fig. 1. Diagrammatic section of the inner incisor of the upper jaw of a Seven-months Fœtus. The loose enamel organ is indicated by * * * *.

Fig. 2. A cusp of the posterior molar, upper jaw of the same. The inner outline represents it before the addition of acetic acid—the outer afterwards, when Nasmyth's membrane is seen raised up into large folds.

Fig. 3. Edge of an incisor pulp—retaining its cap—not far from the lower edge of the dentine, which was about 1-1600th of an inch thick.

Fig. 4. Edge of the pulp of a molar cusp, showing the first rudiment of the dentine, commencing in a perfectly transparent layer between the "nuclei" of the pulp and the membrana preformativa.

Fig. 5. Surface of this dentine, where it had attained a thickness of 1-2500th of an inch, before which the little cavities, if present, were not visible.

Fig. 6. Nasmyth's membrane detached from the subjacent enamel by acetic acid.

Fig. 7. The "stellate-cells" of the human "enamel-organ."

Fig. 8. Tooth of the Frog, acted on by dilute hydrochloric acid, so as to dissolve the enamel and free Nasmyth's membrane. The structure of the dentine is rendered indistinct. At the base Nasmyth's membrane is continued over the bony substance at *z*, in which the nuclei of the lacunæ are visible.

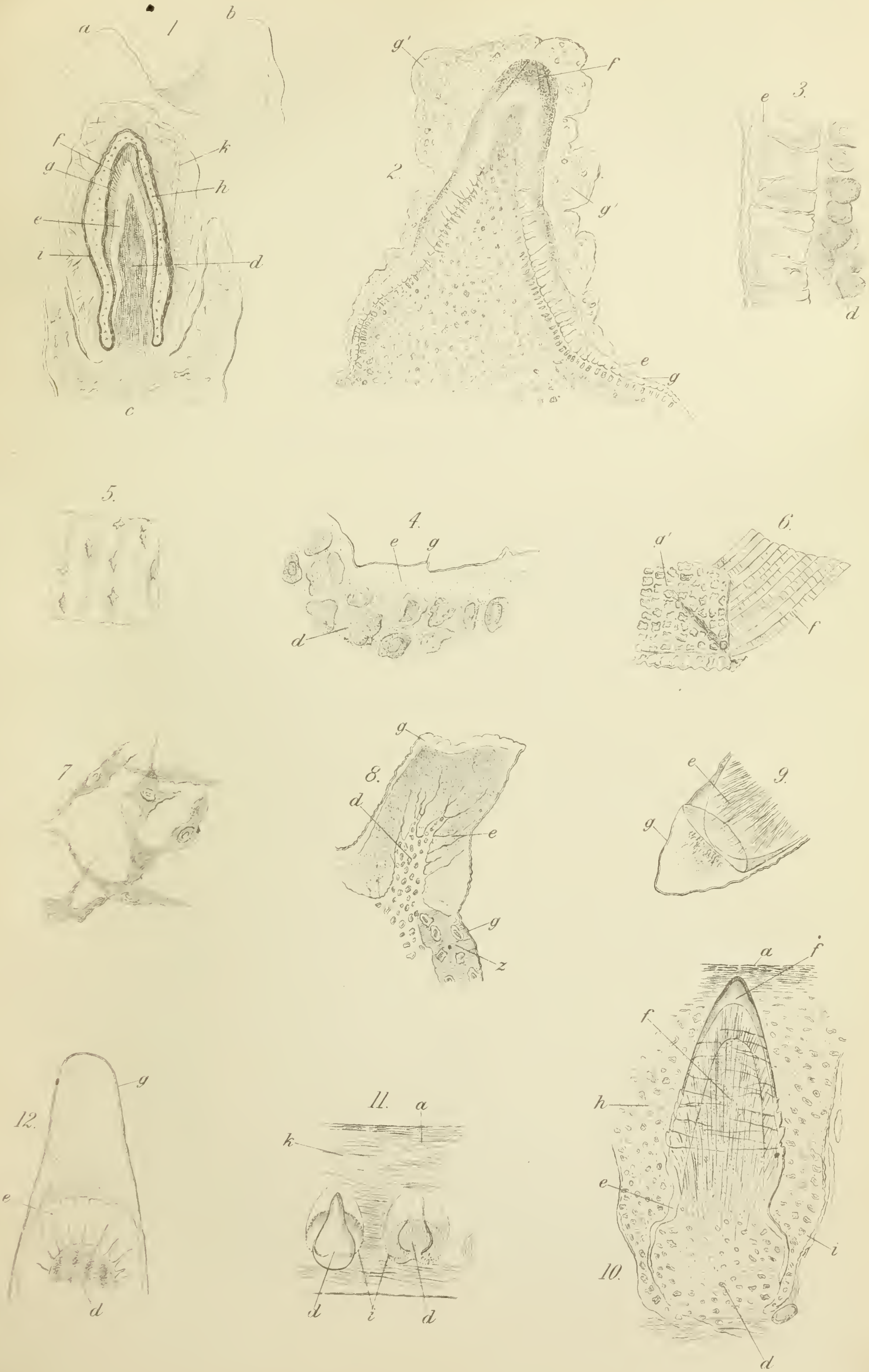
Fig. 9. Extremity of the tooth of a Mackerel, acted on by hydrochloric acid so as to dissolve the enamel. Nasmyth's membrane is rendered obvious, but is burst on the left-hand edge.

Fig. 10. Tooth-sac of a Mackerel, 1-50th of an inch long, extracted from its alveolus. Its close resemblance to a hair-sac is very striking.

Fig. 11. Diagrammatic section of the dental follicles of a Skate, to show the union of the upper and lower folds of the "dental groove."

Fig. 12. Extremity of a dermic, tooth-like spine, from the upper surface of the head in the Skate, acted on by hydrochloric acid, which has removed the layer of enamel.

[PLATE XXIII]



T.H.H. del[t]

XXIII

THE CELL-THEORY

Brit. and For. Medico-Chir. Review, vol. xii., 1853, *pp.* 285-314.

REVIEW I.

1. *De Partibus Similaribus.* By G. FALLOPIUS. (Date uncertain, before 1562.)
2. *Theoria Generationis.* By CASPAR FRIEDRICH WOLFF. 1759.
3. *Theorie von der Generation.* By C. F. WOLFF. 1764.
4. *Theoria Generationis.* By C. F. WOLFF. Ed. Nova. 1774.
5. *Von der eigenthümlichen und wesentlichen Kraft der Vegetabilischen sowohl als auch der animalischen Substanz.* By C. F. WOLFF. 1789.
6. *Entwickelungs Geschichte d. Thiere.* By K. E. VON BAER. 1828.
7. *Untersuchungen über Phytogenesis.* By SCHLEIDEN. 1837.
8. *Mikroskopische Untersuchungen.* By SCHWANN. 1838–9.
9. *Ueber das Bindegewebe.* By REICHERT. 1845.
10. *Die Vegetabilische Zelle.* By H. VON MOHL. 1850.

The Vegetable Cell. By H. VON MOHL. Translated by A. HENFREY, F.R.S. 1852.

11. *On the Mutual Relation of the Vital and Physical Forces.* By W. B. CARPENTER, M.D., F.R.S., &c. ('Phil. Trans.') 1850.
12. *Handbuch der Gewebelehre.* By A. KÖLLIKER. 1852.

IF we separate the elementary and essential facts of Life from all the various and complicated phenomena with which they are associated among the higher forms of living beings—if we examine those lowest and most rudimentary states of animal and vegetable existence, which are presented to us by the so-called 'unicellular' organisms, we find that the sole definable difference between a living thing and a mere formed morsel of some protein compound, fresh from the laboratory of the chemist, is, that while the protein compound undergoes no change which may not be traced to the immediate and direct operation of some new or varying external condition, the Navicula or the Gregarina passes through the most remarkable successions of form, of size, and of chemical composition, which are equally definite in their nature, and equally certain in the order of their occurrence,

whatever, within certain limits, be the change in external conditions, or whatever pains may be taken to prevent any variation in them.

Broadly, we may thus state the difference between the subjects of Physical and those of Biological Science: the former, the stone, the gas, and the crystal, have an *inertia;* they tend to remain as they are, unless some external influence affect them. The latter, animals and plants, on the other hand, are essentially characterized by the very opposite tendencies. As Reichert well expresses it:

"All organic bodies, therefore, represent, in relation to one another different and manifold states succeeding one another definitely upon a similar and homogeneous foundation; they form a common differential series, in which, *independently of external conditions*, a continual increase in the mutual differences and a diminution of the resemblances, occur." (p. 12.)

Linnæus seems to have wished to express his insight into this difference between living and dead matter, in his celebrated aphorism: "Stones grow; plants grow and live;" but so long as this "and live" was not analysed into its true meaning, the phrase marked the difference, but failed to define it.

Bichât recognised the independence of action of living beings in another way. All things which surround living beings tend, he says, to destroy them; but they nevertheless follow out their own appointed course. "La vie est l'ensemble des fonctions qui resistent à la mort." [1]

Now, this faculty of pursuing their own course, this inherent law of change, introduces, it will be observed, an element into the study of living beings which has no analogue in the world of ordinary matter. The latter frequently possesses structure, and may therefore be the legitimate subject of anatomy; but it undergoes no definite cyclical alterations,[2] and, therefore, it offers nothing which corresponds

[1] It is amusing to find M. Comte, a mere bookman in these subjects, devoting a long argument (Philosophie Positive, tom. iii. p. 288) to a refutation (?) of what he calls the "profonde irrationalité" of Bichât's definition. As a specimen of the said refutation, we may select the following passage: "Si comme le supposait Bichât, tout ce qui entoure les corps vivans tendait réellement à les detruire, leur existence serait par cela même radicalement inintelligible; car, où pourraient-ils puiser la force nécessaire pour surmonter même temporairement un tel obstacle?" What a question for a positive philosopher! Does M. Comte doubt his own power to get up from his easy chair, because it is unquestionably true that the action of the whole globe "tends" to retain him in his sitting posture, and because he cannot tell whence he gets the force which enables him to rise?

[2] It is not easy to frame a definition of the differences between living and not living bodies which shall perfectly defy cavil. That in the text—based on the inertia of not living bodies, the internal activity of living bodies—marks the difference strongly but not unobjectionably, for it might be said that a nebula undergoing change would, by this definition, be a living body, and in the next place, it might be urged, how do we know that the activity

with what in living beings is called the History of Development, that branch of the investigation of structure which does not concern itself with the mere study of one state of a being—like anatomy—but examines into the manner in which the successive anatomical states are related to, and proceed out of, one another.

A profound physiologist and thinker, a contemporary and worthy rival of Haller, has beautifully expressed the relation of anatomy, of physiology, and of development (which he calls Generation), in the following words:

"The relations between anatomy, the doctrine of generation, and physiology, are about these. By anatomy we learn from observation the composition and structure of an organized body. We, however, are unable to explain this composition and structure; we only know that they are thus, and further than this we know nothing. But now, on the one hand, comes the doctrine of generation, in which that which we know from anatomy historically, is traced to its causes; on the other hand, we have physiology, in which the actions which an organized body is capable of producing are explained. Physiology is related to anatomy exactly as the corollary to the theorem from which it is deduced; my theory (of generation) is related to anatomy as its demonstration to the theorem." [1]

And again we find the relation of development to anatomy admirably and epigrammatically expressed in the 'Theoria Generationis' of the same writer. Development is, he says, "anatomia rationalis."

It has been said, and without doubt with profound truth, that the study of the structure of living beings originated in the wonder excited by their actions. But though this may, nay, must, have been the case at first, and though the curiosity of man has for three centuries past directed itself, with almost equal impartiality, to physiological,

of living bodies is not really the result of some external cause with which we are unacquainted? It might be said, that the apparent absence of change in external conditions, is no more evidence that the vital phenomena are independent of some such causes, than the continuous running of a stream when the dam is opened, independent of any further alteration of external conditions, is evidence of spontaneity. The action of the spermatozoon, e.g., might be compared to the raising of the dam. We have preferred above, however, a vivid to an exact definition of our conception of life, as likely to be more useful. If we were to attempt an exact definition, it would be, that a living being is a natural body which presents phenomena of growth, of change of form, and of chemical composition, of a definite nature, and occurring in definite cycles of succession. This definition will separate living beings from all other terrestrial bodies. It separates them from cosmical bodies (nebulæ, &c.) only by the nature of the phenomena which succeed one another; so true is it that the microcosm and the macrocosm are reflections of one another.

[1] Wolff: Theorie von der Generation, p. 12.

anatomical, and developmental inquiries, still it is clear, that if the above account of the correlation of these branches of science be correct, their logical connexion, and the order, therefore, in which they must eventually arrive at perfection, is precisely the reverse. The striking and mysterious character of many of the functions may have led to the study of structure; but assuredly the understanding of the former presupposes a thorough knowledge of the latter.

It is conceivable that structure might be thoroughly made out without the least acquaintance with function, just as the ancient anatomists were well acquainted with the construction of the muscular system, and yet had no suspicion of its being the motor apparatus, and as at the present day we know full well the structure of the "vascular glands," though we can but guess their purpose; but it is quite impossible to attain to a complete knowledge of function without a thorough anatomical analysis. The action of the whole of any organ depends upon and is, that of the sum of its parts; it is, mechanically speaking, their resultant; so that until the nature and the precise modes of operation of all these parts have been made out, we can have no security that any law propounded concerning the functions of the whole, is other than a mere empirical generalization, liable to be interfered with at any moment, by the properties of some of the elementary parts with which we are unacquainted. Thus, up to within a few years ago, contractility was affirmed to be a general property of the cellular tissue of the skin; and this would have remained as an ascertained law, had not Kölliker shown, by the discovery of the extensive distribution of muscular fibre in it (that is, by pushing anatomical analysis a step further than it had previously been carried), that the supposed law was but an empirical generalization, and that the property of contractility, supposed to be inherent in the ordinary connective tissue of the skin, was, in fact, deducible from the presence of a totally different structure.

So again, Haller and his followers quoted the contraction of the heart, when removed from the body, as evidence of the innate contractility of muscle, apart from all nervous influence. This *vis insita* may exist or it may not, but further anatomical investigation has at any rate destroyed the force of the argument, by demonstrating the existence of nervous ganglia within the substance of the organ.

But enough of illustration of what must be sufficiently plain to any one who will reflect upon the subject; namely, that however much might be done towards the establishment of broad physiological truths, while the knowledge of structure was in a rough and imperfect state, still an exhaustive study of structure is absolutely necessary,

before any successful attempt can be made to establish the true laws of function, or to build the science of physiology upon an exact foundation.

Herein lies, consciously or unconsciously to their authors—for the man of genius is such, in virtue of having true and just tendencies and impulses, of which he often can give himself no logical account—the secret of the repeated attempts which have been made from the time of the very fathers of biology, to found what we now call the doctrine of general anatomy or histology, which is, in other words, the exhaustive anatomical analysis of organized bodies. That animals and plants, complex as they may appear, are yet composed of comparatively few elementary parts, frequently repeated, had been noticed by the profound intellect of Aristotle; and Fallopius tells us that Galen had attained to still more clear and definite conceptions with regard to these "partes similares" or "simplices."[1]

"Galenus per simplices partes eas intelligit quæ non constant ex dissimilibus substantiis, in quas resolvitur corpus humanum, nec ultra datur progressio et istæ partes dicuntur simplices quia cum ad hoc ventum fuerit in resolutione corporis humani, non amplius progredi possumus." (p. 103.)

Such, indeed, must be the definition of elementary parts at all periods of science—they are ultimate, because we can go no further; though it is of course a very different matter whether we are stopped by the imperfection of our instruments of analysis, as these older observers were, or by having really arrived at parts no longer analyzable.

The celebrated professor of Modena, whose words we have just cited, was one of the first of those who carried the light shed by the revival of letters into the region of medicine and its allied sciences; and his work 'De Partibus Similaribus,' from which they are taken, must excite the admiration of every modern reader, not merely by the critical acumen and original genius which it displays, but by the scientific and absolutely accurate manner in which the whole subject of general anatomy is handled.

The classes of "partes similares," or tissues, of which he treats, are bone, cartilage, fat, flesh, nerve, ligament, tendon, membrane, vein, artery, nails, hairs, and skin; and he examines and details under each head the minute structure, so far as it was accessible to his means of investigation; the chemical and physical properties (expressed, of course, in the language of the day), and even the peculiarities

[1] Terms by no means always convertible, but which may for the present be taken to be so.

manifested by the diseased state. Nor is he at all wanting in what has been considered, and justly, to be Bichât's great merit—an essentially *positive* method of studying the tissues, inasmuch as he particularly insists on the necessity of investigating the properties of each tissue for itself, and of avoiding all hypothetical speculation; in fact, with the quaint plainness of the age, he does not hesitate to insinuate that Averrhöes must have been "ebrius" when he discoursed touching "spiritus qui insensibiles sunt."

The vitality of each tissue, independently of every influence save the general conditions of nutrition, is maintained by Fallopius, not as a mere speculation, but on sound embryological grounds. How can the liver, he asks, be the sole source and prime mover of all vital organization, as some have maintained, when, in the development of the chick, we see other organs appear before it? All that the liver and the vessels can do is to modify the supplies, by affecting the "restitutiones spirituum ac nutrimentis" (p. 98), the "partes similares" themselves having a "regimen insitum," or, as in our day it would be called, "vital force," of their own; and he quotes, as expressing his own views, the following remarkable passage from Actuarius:

"Quod partes naturales agunt propriâ formâ ac cum instrumento quod dicitur spiritus animalis: nam hoc instrumento per propriam formam attrahunt, concoquunt et expellunt, et hic spiritus est immediatum instrumentum vis naturalis, et hic spiritus dicit Actuarius, *originem ducit unâ cum formâ ipsius particulæ, et ex eâdem materiâ eodemque tempore fit.*"

Substitute here for the indefinite "particulæ" definite vesicular particles or cells, and for "spiritus animalis" the modern terms of equivalent meaning or no meaning—vital-force or cell-force, and this passage would serve very well as a concise expression of the "cell-theory," such as may be found in many a hand-book of the day. So far, and no further, have three centuries brought us!

In fact, it must be confessed, that these old writers were fully possessed (more so, in truth, than many of their successors) with the two fundamental notions of structural and physiological biology; the first, that living beings may be resolved anatomically into a comparatively small number of simple structural elements; the second, that these elementary parts possess vital properties, which depend for their manifestation only upon the existence of certain general conditions (supply of proper nutriment, &c.), and are independent of all direct influence from other parts.

But it would seem, that Truth must pass through more than one Avatar, before she can attain a firm hold upon the mind even of men

of science—and at the end of the eighteenth century it required all the genius of Bichât to sift the wheat from the chaff, amongst the great mass of facts which the observation of the past ages had accumulated—and strengthening whatever place was weakest by new investigations—to establish these very two propositions, upon a broad and henceforward firm foundation. Great as was the service which Bichât rendered in this way to biology—and wide as the difference between the treatise 'De Partibus Similaribus' and the 'Anatomie Generale' may be—still the one is the intellectual progeny of the other, and exhibits neither alteration nor improvement in the method pursued.

In the meanwhile, however, an aid to investigation had arisen, by the means of which this method could be pushed to its uttermost limits—we refer to the invention of the microscope. The influence of this mighty instrument of research upon biology, can only be compared to that of the galvanic battery, in the hands of Davy, upon chemistry. It has enabled *proximate* analysis to become *ultimate*. Without the microscope the ultimate histological elements were, as we have seen, defined *negatively*, as parts in which any further structural difference was too small to be detected. The microscope, on the other hand, enables us to define the tissues *positively*—to say, a given tissue has such a structure, and magnify it as you will, it will present no further differences.

The amount of such positive information as to the ultimate structure of the tissues, collected by Leuwenhoek, Malpighi, and their successors, between the middle of the seventeenth and the fourth decade of the present century, was very great, and in fact the most important and characteristic features presented by the histological element of plants and animals may be said to have been well made out, at the time of the appearance of the celebrated treatises by Schleiden and Schwann, cited at the head of this article; and these writers, therefore, added but little to the body of knowledge in this direction. It is most unquestionable, however, that the biological sciences, and more especially histology, received a wonderful stimulus at their hands. Whatever cavillers may say, it is certain that histology before 1838 and histology since then, are two different sciences—in scope, in purpose, and in dignity—and the eminent men to whom we allude, may safely answer all detraction by a proud "*circumspice*."

But wherein does the real value of their work lie? We think this question may be readily enough answered by those who admit the force of what has been said in our opening paragraphs—who acknowledge that mere anatomy does not exhaust the structure of living beings—and that before histology can be said to be complete, we must

have a histological *development* as well as a histological *anatomy*. Leuwenhoek and the majority of his successors had enough to do in making out the "*historicam cognitionem*," the simple anatomy of the tissues; it tasked all their powers to arrive at a clear statement of the "*theorem*," while it is the great merit of Schleiden and Schwann that they sought to arrive at an "*anatomia rationalis*," and to furnish the "demonstration of the theorem." The old method of investigation had been carried as far as it would go, and they applied the only other which remained, and made it familiar to the general mind. Turn to any of Schleiden's works, and we find the logical acuteness, and the vituperative sarcasm, which he wields with equal force, employed in urging the study of development as the one thing needful for scientific botany. And Schwann's entire essay testifies to what he expressly tells the reader, that his investigations are distinguished from all others by being based upon the study of development. Let one citation suffice:—"The theory of the present investigation was, therefore, to show . . . . that there exists a common principle of development for all the elementary parts of the organism." (Schwann, pp. 193—196.)

Intending as we do to venture upon a critical examination of the absolute value of Schleiden's and Schwann's contributions to biological science, which may lead us to conclusions not ordinarily admitted, we have been particularly desirous to estimate fairly the position which they occupy in its history, and the influence which their labours have had upon its progress—which is a widely different matter—for, in attempting to weigh the labours of others, we should be in danger of committing great injustice, if we did not carefully bear in mind that paradoxical as it may seem, the value of a theory and its truth, are by no means commensurate. In so complex a science as that which relates to living beings, accurate and diligent empirical observation, though the best of things as far as it goes, will not take us very far; and the mere accumulation of facts without generalization and classification is as great an error intellectually, as, hygienically, would be the attempt to strengthen by accumulating nourishment without due attention to the primæ viæ, the result in each case being chiefly giddiness and confusion in the head.

In biology, as in all the more complicated branches of inquiry, progress can only be made by a careful combination of the deductive method with the inductive, and by bringing the powerful aid of the imagination, kept, of course, in due and rigid subordination, to assist the faculties of observation and reasoning; and there are periods in the history of every science when a false hypothesis is not only better

than none at all, but is a necessary forerunner of, and preparation for, the true one. As Schwann himself well expresses it :

" An hypothesis is never hurtful, so long as one bears in mind the amount of its probability, and the grounds upon which it is formed. It is not only advantageous, but necessary to science, that when a certain cycle of phenomena have been ascertained by observation, some provisional explanation should be devised as closely as possible in accordance with them ; even though there be a risk of upsetting this explanation by further investigation ; for it is only in this way that one can rationally be led to new discoveries, which may either confirm or refute it." (p. 221.)

The value of an hypothesis may, in fact, be said to be twofold—to the original investigator, its worth consists more in what it suggests than in what it teaches ; let it be enunciated with perspicuity, so that its logical consequences may be clearly deduced, and made the base of definite questions to nature—questions to which she must answer yes or no—and of its absolute truth or falsehood, he recks little : for the mass of men, again, who can afford no time for original research, and for the worker himself, so far as respects subjects with which he is not immediately occupied, some system of artificial memory is absolutely necessary. This want is supplied by some " appropriate conception " which, as Dr. Whewell would say, " colligates " the facts—ties them up in bundles ready to hand—by some hypothesis, in short. Doubtless the truer a theory is,—the more "appropriate " the colligating conception,—the better will it serve its mnemonic purpose, but its absolute truth is neither necessary to its usefulness, nor indeed in any way cognizable by the human faculties. Now it appears to us that Schwann and Schleiden have performed precisely this service to the biological sciences. At a time when the researches of innumerable guideless investigators, called into existence by the tempting facilities offered by the improvement of microscopes, threatened to swamp science in minutiæ, and to render the noble calling of the physiologist identical with that of the 'putter-up' of preparations, they stepped forward with the cell-theory as a colligation of the facts. To the investigator, they afforded a clear basis and starting-point for his inquiries ; for the student, they grouped together immense masses of details in a clear and perspicuous manner. Let us not be ungrateful for what they brought. If not absolutely true, it was the truest thing that had been done in biology for half a century.

But who seeks for absolute truth ? Flattering as they were to our vanity, we fear it must be confessed that the days of the high *a priori* road are over. Men of science have given up the attempt to soar

eagle-like to some point amidst the clouds, whence the absolute relations of things could be securely viewed ; and at present, their more useful, if more ignoble course, may rather be compared to that of the flocks of sparrows in autumn, which one sees continually halting, yet always advancing—flying from tree to tree, noisily jubilating in each, as if that were assuredly the final resting-place and secure haven of sparrows, and yet as certainly taking their departure after awhile, in search of new acquisitions. We must build our theories, in these days, as we do our houses : giving up all attempt at Cyclopean architecture, let us bethink ourselves rather of the convenience of our successors, who will assuredly alter, and perhaps pull them down, to suit the needs of their own age ; and if we seek their gratitude, let us strive not so much to knit our materials firmly together (which will only give them more trouble and yield us less thanks), as to see that they are separately sound and convertible. This much digression has seemed necessary, by way of securing ourselves from any suspicion of a desire to under-estimate the historical value of Schleiden and Schwann's researches, in the course of an attempt to show that they are based upon errors in anatomy, and lead to errors in physiology.

Again, with regard to that value, we have a few words to say in a merely historical point of view. The sketch we have given of the progress of general anatomy, we believe, omits mention of no ordinarily recognized epoch, nor fails to indicate the acknowledged order of the successive introduction of those great leading ideas with which we are at present concerned.[1] In their own belief, and in that of their contemporaries, Schleiden and Schwann have not only worked out developmental histology, but originated it ; and the latter, in his reclamation against Valentin (loc. cit., pp. 260, 261), defends his claim to be considered the originator of the idea that " a common principle governs the development of the elementary parts of all organisms." Now, we fully recognise the originality of these writers ; we believe that they deserve all the credit which can attach to a noble plan carried out with no small success ; and we further remember that the majority always sympathizes with the cry, " Pereant qui ante nos, nostra," &c. ; but, as we have said, truth often has more than one Avatar, and whatever the forgetfulness of men, history should be just, and not allow those who had the misfortune to be before their time, to pass for that reason into oblivion.

Such was the position into which his great genius forced Caspar

[1] Compare Kölliker's Handbuch, Introduction ; or Sprengel's Geschichte der Arzneykunde.

Friedrich Wolff—such the fate with which he has met. The manuals of physiology tell us that he was the founder of the doctrine of epigenesis—a doctrine which, in the present day, seems so plain and obvious, that we do not give him much credit for it, forgetting that he had to struggle against the authority of Malpighi and of Haller, and the attacks of Bonnet ; influence and authority so great, that though every reader of the 'Theoria Generationis' must see that Wolff triumphantly establishes his position, yet, seventy years afterwards, we find even Cuvier [1] still accrediting the doctrine of his opponents.

It is less generally (we might say hardly at all) known that Wolff demonstrated, by numerous observations on development, the doctrine of the metamorphosis of plants, when Göthe, to whom it is commonly ascribed, was not quite ten years old ; [2] but it seems to have been wholly forgotten that he endeavoured to work out, upon the basis of the strict study of histological and morphological development, that "identity of structure of plants and animals" which is the thesis defended by Schwann. Had Wolff's teaching been founded upon one of those clever guesses upon which an able man will often build up a plausible hypothesis, we should have thought it quite unnecessary to make even historical reference to him ; but the most cursory examination of the 'Theoria Generationis,' or of the more popular and discursive exposition of his views in the 'Theorie von d. Generation,' is enough to dispel any such notion. The passage we have already quoted is sufficient to show how just and accurate Wolff's ideas upon the importance of the study of development, as a method, were ; and the whole of his work is the laborious application of that method. The parts of the calyx, of the corolla, and of the pericarp, are for him "modified leaves ;" not because certain observed modifications had suggested that they might be so considered—which is the whole gist of Göthe's subsequent argument—but because he had carefully traced back their development, and had found that they all proceeded from the same original form. The homology of the wing of the chick with its leg is placed by Wolff on precisely the same basis—the only one, be it observed, on which any homology can ultimately rest ; and following out the argument to its legitimate conclusion, he shows that the appendicular organs of plants and animals are developed after the

[1] Histoire des Sciences Naturelles.

[2] The world, always too happy to join in toadying the rich, and taking away the "one ewe lamb" from the poor, persists in ascribing the theory of the metamorphosis of plants to Göthe, in spite of the great poet himself (see Göthe's Werke, Cotta, 1840, B. 36, p. 105 : "Entdeckung eines trefflichen Vorarbeiters"), who not only acknowledges his own obligations to Wolff, but speaks with just wonder and admiration of the 'Theoria Generationis,' the work of a young man of six-and-twenty.

same fashion. The limbs of animals, he says, are developed in the same manner from the body of the embryo, as the leaf from the stem, or the lamina of the leaf from its mid-rib. Ordinary four-footed animals are like pinnatifid leaves, while "the bat is a perfect leaf—a startling statement, but, as I have shown, the analogy is not chimerical for the *mode of origin of the two is the same*." [1]

Wolff's doctrine concerning histological development is shortly this.[2] Every organ, he says, is composed at first of a little mass of clear, viscous, nutritive fluid, which possesses no organization of any kind, but is at most composed of globules. In this semi-fluid mass, cavities (*Bläschen*, *Zellen*) are now developed; these, if they remain rounded or polygonal, become the subsequent cells—if they elongate, the vessels; and the process is identically the same, whether it is examined in the vegetating point of a plant, or in the young budding organs of an animal. Both cells and vessels may subsequently be thickened, by deposits from the "solidescible" nutritive fluid. In the plant, the cells at first communicate, but subsequently become separated from one another; in the animal, they always remain in communication. In each case, they are mere cavities, and not independent entities; organization is not effected by them, but they are the visible results of the action of the organizing power inherent in the living mass, or what Wolff calls the *vis essentialis*. For him, however, this "vis essentialis" is no mythical *archæus*, but simply a convenient name for two facts which he takes a great deal of trouble to demonstrate; the first, the existence in living tissues (before any passages are developed in them) of currents of the nutritious fluid determined to particular parts by some power which is independent of all external influence; and the second, the peculiar changes of form and composition, which take place in the same manner.

Now there is really no very great difference between these views of the mode of development of the tissues and those of Schleiden and Schwann. The "solidescible nutritive fluid" of Wolff is the "cytoblastema" of Schleiden and Schwann; with the exception of the supposed relation of the nucleus to the development of the cell (which, as we shall see, is incorrect) Wolff's description of the latter process is nearly that of Schleiden; Wolff maintains that the "vessels" of plants are the result of the greater activity of the nutritive currents in particular directions; and so does Schleiden.[3]

[1] Theorie von der Generation, § 64.

[2] Theoria Generationis, and Von der eigenthümlichen Kraft, p. 48.

[3] It is very curious to find even Schwann's definition of cell-development as the "crystallization of a permeable body" anticipated by Wolff, Von d. eigenthümlichen Kraft, &c.,

Examining his statements closely, we notice, indeed, that his imperfect means of investigation led Wolff into two important errors —that of supposing the cells of plants to communicate in their youngest state, and thence deducing a false analogy with the areolar tissue of animals ; and that of supposing that animal and vegetable tissues are always, in their very youngest state, absolutely structureless. However, as we shall see subsequently, Wolff is by no means singular in having started with grave anatomical mistakes, and we cannot perceive that in his case these errors, one of which, at any rate, Schleiden shares with him, vitiate those other and more important parts of his views, to which we are about to refer.

We have said, in fact, that not merely speculatively, but by observation, Wolff established a theory of the development of the vegetable tissues very similar to that of Schleiden, and that "identity of structure as shown by their development," between plants and animals, to prove which, was the purpose of the microscopical investigations of Schwann. But he did much more than this. In the 'Theoria Generationis,' and in the essay on the vital forces published thirty years afterwards, Wolff developed some very remarkable views on the relation of life to organization—of the vital processes to the organic elements—in which he diverges very widely from all who preceded, and from most who have followed him, most of all from Schleiden and Schwann. We may best exhibit the bearing of these views by contrasting them with those of the latter writers.

Schleiden and Schwann teach implicitly that the primary histological elements (cells) are independent, anatomically and physiologically ; that they stand in the relation of *causes* or *centres*, to organization and the "organizing force ;" and that the whole organism is the result of

p. 63 : ". . . . . so, from the case of many other attractions, especially of crystallization, which, among all known phenomena, comes nearest to vegetation, that without the second property—viz., that by means of which the mutually attractive substances interpenetrate and mingle with one another—the attractive force, although it should possess the first property, yet could as little effect nutrition. The particles of a salt dissolved in water attract only particles of salt—i.e., homogeneous substances, and repel all heterogeneous matters ; for we get pure (crystals of the) salts. But out of this attraction comes nothing that can be compared with nutrition ; for although the whole mass of substance is increased by degrees, yet crystals once formed remain as they are, and are not increased in their substance, and nothing less than the formation of new organization and continual change of figure accompanies this increase. . . . . Crystals once formed attract the saline particles only to their outer surface, upon which the attracted parts are deposited. They do not attract these particles into their substance. . . . . If the saline particles, on the other hand, penetrated the crystals and increased their substance homogeneously in all parts, this process would be indistinguishable from nutrition, and would consequently be a true nutrition." Compare Schwann, pp. 239—257.

the union and combined action of these primarily separate elements. Wolff, on the other hand, asserts that the primary histological elements (cells too, but not always defined in the same way) are not either anatomically or physiologically independent; that they stand in the relation of *effects* to the organizing or vital force (vis essentialis); and that the organism results from the "differentiation" of a primarily homogeneous whole into these parts. Such a doctrine is, in fact, a most obvious and almost a necessary development of the doctrine of epigenesis in general. To one who had worked out the conclusion, that the most complex, grosser, animal or vegetable organizations, arise from a semi-fluid and homogeneous mass, by the continual and successive establishment of differences in it, it would be only natural to suppose that the method of nature, in that finer organization which we call histological, was the same; and that as the organ is developed by the differentiation of cells, so the cells are the result of the differentiation of inorganic matter. If the organism be not constituted by the coalescence of its organs and tissues in consequence of their peculiar forces, but if, on the other hand, the organism exists before its organs and tissues, and evolves them from itself,—is it not probable that the organs and tissues also, are not produced by the coalescence of the cells of which they are composed, in consequence of *their* peculiar forces, but, contrariwise, that the cells are a product of the differentiation of something which existed before them?

For Schwann the organism is a beehive, its actions and forces resulting from the separate but harmonious action of all its parts (compare Schwann, l. c., p. 229). For Wolff it is a mosaic, every portion of which expresses only the conditions under which the formative power acted and the tendencies by which it was guided.

We have said above, not without a full consciousness of the responsibility of the assertion, that we believe the cell-theory of Schleiden and Schwann to be based upon erroneous conceptions of structure, and to lead to errors in physiology, and we beg now to offer some evidence in favour of these views. We need not stop to prove, what must be familiar to every one who is acquainted with Schwann's work, that in making his comparison of animal with vegetable structures, he rests wholly upon Schleiden's statements concerning the development, and upon the commonly prevalent views with respect to the anatomy, of the latter.

It is clear, then, that however logically consequent Schwann's work may be in itself, its truth and the justice of its nomenclature will depend upon that of these latter views and statements. Schwann took these

for granted, and if they were untrue he has been trusting to a rotten reed. Such, we fear, has indeed been the case. Schwann's botanical data were:

1. The prevalent notion of the anatomical independence of the vegetable cell, considered as a separate entity.
2. The prevalent conception of the structure of the vegetable cell.
3. The doctrine of the mode of its development.

Each of these, as assumed by Schwann, and as taught by Schleiden, has since, we shall endeavour to show, been proved to be erroneous. We will take them *seriatim*.

1. The first observer who, aided by the microscope, turned his attention to the structure of plants, was the versatile Hooke, and, as might be expected, the most noticeable thing to his mind was the existence of the innumerable cavities or "cells" scattered through their substance. Malpighi, the first proper botanical histologist, found that the walls of these vesicles were separable, that they could be isolated from one another, and therefore, doubtless urged more by the obvious convenience of the phraseology, than by any philosophical consideration upon the subject, he gave each the definite name of "utriculus," and regarded it as an independent entity. Of course it was a natural consequence that the plant should be regarded as constituted by the *union and coalescence* of a great number of these entities.

Grew, who if all scandal be true, is so much indebted to Malpighi, did not appropriate this view among other things; on the other hand, he compared the utricles to the cavities in the foam of beer; and subsequently Wolff propounded the idea, that the cells were cavities in a homogeneous substance, as we have mentioned above. In modern times, the most important defender of this mode of regarding the matter has been Mirbel, who (escaping the error of Wolff, that the cavities of the cells communicate) endeavoured to demonstrate its truth, by tracing the formation of the cambium; but, at the time when Schwann wrote, it must be considered to have been wholly discredited, the opposite view having one of its strongest supporters in the caustic Schleiden himself—as, indeed, would necessarily be the case, from the tendency of his researches upon phytogenesis. As we shall see below, however, Schleiden was quite wrong in his ideas of cell-development—and we have therefore merely to consider the purely anatomical arguments for the independence of the cell. Now these amount, however various their disguise, to nothing more than this—that, by certain chemical or mechanical means, a plant may be broken up into vesicles corresponding with the cavities which previously existed in it: of

course no one denies this fact ; but of what value is it ? Is the fact that a rhombohedron of calcareous spar breaks up, if pounded, into minute rhombohedrons, any evidence that those minuter ones were once independent, and formed the larger by their coalescence ? Is the circumstance that wood itself tears up into fibres, any evidence that it was formed by the coalescence of fibres ? Assuredly not ; for every hand-book will tell us that these fibres are the result of a metamorphosis of quite different parts. Is it not perfectly clear, that the behaviour of a body under mechanical or chemical influences, is simply an evidence of the disposition of the lines of greatest cohesion or affinity among its particles *at the time being*, and bears not in the slightest degree upon the question as to what these lines indicate ; whether they are the remains of an ancient separation among heterogeneous parts, or the expression of a recent separation which has arisen in a homogeneous whole ? So that, if the walls of the cells were really, as distinct from one another as is commonly supposed, it would be no argument for their vital independence : but they are not so. Von Mohl has shown that, in the great majority of cases, the assumption of the existence of a so-called intercellular substance, depends simply on imperfect chemical investigation, that there exists no real line of demarcation between one cell and another, and that wherever cells have been separated, whether mechanically or chemically, there is evidence that the continuous cellulose substance has been torn or in some way destroyed. In young tissues—such, for instance, as the cambium, or the base of a leaf, we have been quite unable to detect the least evidence of the existence of any line of demarcation between the cells ; the cellulose substance forms a partition between cavity and cavity, which becomes evenly blue throughout by the action of sulphuric acid and iodine, and which certainly, even under the highest powers, exhibits no symptom of any optical difference ; so that, in this state, vegetable tissue answers pretty closely to Wolff's idea. It is a homogeneous cellulose-yielding, transparent substance, containing cavities, in which lie peculiar vesicular bodies, into whose composition much nitrogen enters. It will be found a great aid if in the present confused state of terminology the reader will accept two new denominations for these elementary parts, which express nothing but their mutual relation. To the former, and to everything which answers to it, we shall throughout the present article give the name of *Periplast*, or periplastic substance ; to the latter, that of *Endoplast*. So far, then, from the utricles or cells in the plant being anatomically distinct, we regard it as quite certain that that portion which corresponds with the periplast, forms a continuous whole through the entire plant.

2. In 1837-8, each utricle of the plant was considered to have the following composition. In the first place, there was the cellulose cell-wall, or the portion of periplast answering to any particular endoplast; secondly, there were the cell-contents, a substance of not very defined nature, which occupied the cavity of the cell; and thirdly, there was the *nucleus*, a body to whose occurrence attention was first drawn, as is well known, by our own illustrious botanist, Robert Brown. He, however, cautiously remarked only its very general occurrence, without pretending to draw any inference from the fact; while Schleiden made the belief in its existence, in all young tissues, the first article of the faith botanical. This is, however, most certainly incorrect; there is no trace of a nucleus in many Algæ, such as Hydrodictyon, Vaucheria,[1] Caulerpa; in the leaf of Sphagnum, nor in young germinating Ferns.[2]

Whatever opinion may be entertained upon this head, there is one point quite certain—the enumeration of the elements of the vegetable-cell given above is incomplete; there being one, and that the most important, which is omitted. We refer to the *primordial utricle*, which was only discovered by Von Mohl in 1844. This is a nitrogenous membrane, which always lies in close contact with the periplast, and forms, in fact, an included vesicle, within which the "contents" and the nucleus lie. Instead, therefore, of the endoplast consisting merely of contents and a nucleus, it is a vesicle containing the two latter, when they exist at all; and they are of subordinate importance, for while, as we have seen, a nucleus and formed contents may be absent in young or even fully formed tissues, the primordial utricle is invariably present in the young structures, and often persists until they have attained their full size. Since, then, the functions of the vegetable "cell" can be effectually carried on by the primordial utricle alone; since the "nucleus" has precisely the same chemical composition as the primordial utricle; and since, in some cases of cell-division, new nuclei are seen to arise in the substance of the endoplast, by a mere process of chemical and morphological differentiation (Von Mohl, l. c., p. 52), it follows, we think, that the primordial utricle must be regarded as the essential part of the endoplast—the protoplasm and nucleus being simply its subordinate, and, we had almost said, *accidental* anatomical modifications.

3. Finally, with respect to Schleiden's observations upon the mode of cell-development, according to which in all cases the new production of vegetable-cells takes place by the development of nuclei, round

[1] On Alex. Braun's authority, Ueber Verjüngung, &c., p. 186.

[2] Henfrey, Linn. Trans. 1853.

which the cell-membrane is deposited, subsequently expanding and becoming separated from the nucleus, so as to form a complete cell; we need only say, that they have been long since set aside by the common consent of all observers; in Von Mohl's words (p. 59): "The whole of this account of the relation of the nucleus to the cell-membrane is incorrect." The fact is, that in by far the greater proportion of cases, new cell-development occurs by the division of the previous endoplasts, and the growth or deposition round them and between them, of fresh periplastic substance. The extent of this process of division will be understood, if we remember that all observers now agree in its being the method by which "cell-development" always occurs, except in the embryo-sac of the Phanerogamia, the sporangia of Lichens and of some Algæ and Fungi. The so-called free cell-development of the latter, however, by no means takes place in accordance with Schleiden's views, but by the development of a cellulose membrane (periplast) around a mass of nitrogenous substance (endoplast), which may or may not contain a nucleus; subsequently increasing, *pari passu*, with the periplast. And it is well worthy of consideration, how far the process deserves any distinction, except in degree, from ordinary cell-division, since the new endoplast is only one portion of that of the parent cell, set aside for the purpose of fresh development, while the rest undergoes no corresponding change. However this may be, it may be regarded as quite certain that, leaving out of view the immediate results of sexual reproduction, the whole of the "cells,"—the entirety of the periplasts and endoplasts—of which a plant, whether it be a moss or an oak, are composed, never are independent of one another, and never have been so, at any period of their existence; but that, while the original endoplast of the embryo-cell, from which the plant sprung, has grown and divided into all the endoplasts of the adult, the original periplast has grown at a corresponding rate, and has formed one continuous and connected envelope from the very first. The ground of his comparison, therefore, is cut away from under Schwann's feet; every statement of Schleiden's on which he relied turning out to be erroneous—as we shall see if we turn to his original comparison of cartilage with a vegetable tissue (pp. 9—17). Schwann, finding in cartilage cavities with more or less distinct walls, in each of which lay a corpuscle, singularly resembling the nucleus of the vegetable-cell; finding also that the cell-wall was close to this corpuscle in the younger parts, more distant from it in the older (p. 24), naturally concluded that he had here, in the animal world, an exact confirmation of Schleiden's supposed discoveries, and of course gave to the corpuscle of cartilage the name of "cytoblast,"

or "nucleus," as indicating its homology with the structure of that name, in the plant.

The primordial utricle was, as we have said, not then discovered in the latter, and of course Schwann was not led to look for anything corresponding to it. Indeed, had he done so, his search would have been unsuccessful, for the young and unaltered cartilage cavity contains the corpuscle, and nothing else. The circumstance, therefore, which Schwann considered to demonstrate the identity of structure of plants and animals—i.e., the correspondence of the cartilage-corpuscle with the nucleus of the vegetable-cell, and of the chondrin-wall with the cellulose-wall, would, if it were really the case, be the widest possible ground of distinction between the two, for it would leave the most important element of the latter, the "primordial utricle," without any homologue in the animal, and totally unaccounted for.

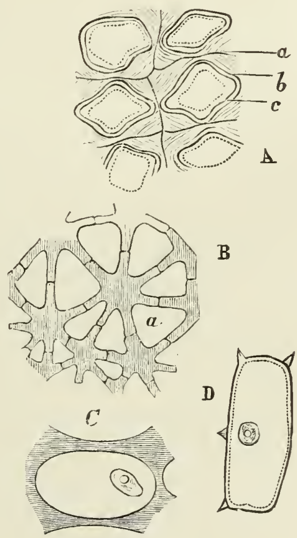


Fig. 1.

A, Collenchyma cells of Beta vulgaris; B, Stellate tissue of the pith of the rush; C, a cartilage-cell with its corpuscle, to compare with D, a vegetable-cell with its nucleus, the primordial utricle in the latter being indicated only by a dotted line.

It is precisely the neglect of this important change in the whole subject, effected by the discovery of Von Mohl, which has, we think, led to the confusion which prevails at present, not only in the comparative, but in the absolute nomenclature of animal histology. Animal physiologists go on using Schwann's nomenclature, forgetting that the whole doctrine of the vegetable-cell, from which he drew that nomenclature, has been completely upset; and at present, beyond the mere fact of a common vesicularity at one period of their existence, one would be led, on opening successively two works on animal and vegetable structure, rather to predicate their total discrepancy, than any uniformity between them.

Now does this discrepancy lie in the facts, or in our names of them? To decide this question, it seemed to us that the only plan was to follow Schwann's steps, and to compare cartilage with a vegetable tissue—for he has shown logically and conclusively enough, that whatever is true of the corpuscle of cartilage, to which he gives the name of "nucleus," is true also of all those corpuscles in the other tissues, to which he gives the same name.

Let us compare, then, some young vegetable tissue, say that of the base of a Sphagnum leaf (fig. 2, A), which is in many respects very convenient for examination, with that of young cartilage (fig. 3, A); the identity of structure is such, that it would be difficult, without the aid of chemical re-agents, to distinguish one from the other: in each, we see highly nitrogenous, more or less vesicular endoplasts imbedded in a homogeneous transparent substance, whose cavities they wholly fill. If we trace the further development, we find that in the Sphagnum leaf the endoplasts and their cavities rapidly increase in size (fig. 2, B), the former becoming, in certain localities of the leaf, regular primordial utricles without any nucleus, and growing in exact proportion to the cavities in the periplast (*b*), while in other directions, having attained a certain size they cease to grow, and rapidly disappear, leaving the periplastic cavity empty (*a*). In cartilage precisely the same thing occurs. The endoplasts increase in size for awhile, and then stop, while the periplastic cavities continue to increase, and thus we have eventually a cartilage-cavity with its corpuscle. In old cartilage the latter frequently disappears, or is converted into fat. We have here purposely selected, in both the animal and the plant, simple cases, in which the endoplast becomes a primordial utricle, without any nucleus. Had we selected the cambium of a phœnogamous plant, it would have been merely necessary to add that, as the endoplast grew, a nucleus appeared in its interior; and in ossifying cartilage, near the ossifying surface, we have repeatedly seen endoplasts such as those described above, some of which contained definite "nuclei," while those in their immediate neighbourhood possessed none.

In the case of cartilage, then (and it is a conclusion at which Leidy and Remak have already arrived), we hold it to be proved that the corpuscle does not correspond with the nucleus of the plant as Schwann supposed, but with the primordial utricle, contents and nucleus; or, in other words, that the "nucleus" of cartilage is the equivalent of the "primordial utricle" of the plant—that they are both endoplasts. It follows, hence, that the chondrin-wall of the cartilage is the homologue of the cellulose wall of the plant, and that they both represent the periplastic element. The phenomena of growth and multiplication exhibited by these corresponding elements are perfectly similar. The process of cell-division, as it is called, is identical in each case. In the plant, the primordial utricles divide, separate, and the cellulose substance grows in between the two. In young cartilage the same thing occurs, the corpuscles divide, separate, and the chondrin substance eventually forms a wall of separation between the two. There is neither endogenous development nor new formation in either case.

The endoplasts grow and divide, the periplast grows so as to surround the endoplasts completely, and except so far as its tendency is, to fill up the space left by their separation, there is no evidence that its growth is in any way affected by them, still less, that it is, as is often assumed, deposited by them. We are led, then, to the conclusion that though Schwann's great principle of the identity of structure of plants and animals is perfectly correct, his exposition of it is incorrect, inasmuch as the corpuscle of cartilage (his "nucleus," whence he reasoned to the other "nuclei") answers not to the "nucleus," but to the "primordial utricle" of the plant; since the mode of development of new "cells," though identical in each case, is different from what Schleiden stated, and Schwann believed; and, finally, since, for the notion of the anatomical independence of the cells, we must substitute that of the unity and continuity of the periplastic substance in each case.

Intimately connected with these structural errors, as we cannot but think them, are Schwann's views of the nature and powers of the "cell," and those subsequently developed (principally by Kölliker) with respect to the action of the nuclei as "centres of force." Led apparently by his views of its anatomical independence, Schwann maintains, as a general proposition, that the cell as such possesses powers which are not inherent in its separate molecules.

"We must, in fact, ascribe an independent life to cells—i.e., the combination of molecules which take place in a single cell are sufficient to set free the force, in consequence of which the cell has the power of attracting new molecules. The cause of nutrition and growth lies not in the organism as a whole, but in the separate elementary parts—the cells. That in point of fact every cell, when separated from the organism, is not capable of further growth as little militates against this theory, as its incapability of existing separate from the swarm would be an argument against the independent life of a bee. . . . . . The inquiry into the fundamental forces of organisms, therefore, is reduced into one concerning the fundamental forces of the single cells." (p. 229.)

And yet, strongly as Schwann maintains, not only here but in many other places, the view that the vital forces are manifested by the cells as machines, and are not inherent in the matter of which these cells are composed, apart from their form; he gives it up in effect when he comes to treat of these forces in detail. The fundamental cell-forces are, he says, of two kinds, the attractive and the metabolic, the former regulating growth, the latter determining the chemical changes; and he shows very justly that these forces are not located in any special centres in the cell, but are exhibited by all its solid constituents (pp.

233, 236), and that they may be exhibited by different portions of these solid constituents, and to a different extent by these different portions (p. 233); proving hereby, very clearly, as it seems to us, that the forces in question are not centralized in the cells, but are resident in their component molecules. All Schwann's able comparison of cell-development with crystallization tends, in fact, to the same conclusion. When matter crystallizes from a solution, the presence of a foreign body may determine the place and form of the deposit; but the crystals themselves are the result, not of the attractive forces of the foreign body, but of the forces resident in their component molecules. So in cell-development, if it is to be rigorously compared to crystallization, even if the nuclei represent the foreign bodies, which determine the place of the chemical and morphological alterations in the surrounding substance, it by no means follows that they are their cause.

Kölliker (§§ 11, 13), resting especially upon the phenomena of yelk-division and of endogenous cell-development, advocates the existence of a peculiar molecular attraction proceeding from the nucleolus first, and subsequently from the nucleus. Now as regards endogenous cell-development, we must confess that we can find no more ground for its occurrence among animals than among plants. Nägeli's cell-development around portions of contents, upon which Kölliker lays so much stress, is nothing more than a case of division of the endoplast (primordial utricle) and subsequent development of periplastic substance round the portions. In cartilage, which is so often quoted as offering marked endogenous cell-development, we must agree with Leidy and Remak, that nothing but division of the endoplasts (nuclei, primordial utricles) and ingrowth of the periplast (intercellular substance, cell-wall) occurs. In these endoplasts again, the very existence of a nucleus is in the highest degree variable and inconstant, and division occurs as well without it as with it.

The process of yelk-division—that remarkable manifestation of a tendency to break up, in the yelk of most animals, into successively smaller spheroids, in each of which a nucleus of some kind appears—seems, at first, to offer very strong evidence in favour of the exertion of some attraction by these nuclei upon the vitelline mass. But we think that a closer examination completely deprives this evidence of all weight. In the first place, the appearance of the nuclei is in many cases subsequent to segmentation. It is thus in Strongylus auricularis (Reichert), in Phallusia (Krohn), in the hen's egg (Remak). In the second place, it seems difficult to conceive any mode of operation of a central attractive force which shall give rise to the phenomena of segmentation, for the resulting spheroids always pass into one another

by extensive plane surfaces, whereas the even action of two attractive centres, in a mass free to move, would give rise to two spheroids in contact only by a point. Again, Remak has observed that in the frog's egg the time occupied by the formation of the groove, indicating the first line of cleavage upon the upper half of the yelk, is very much shorter than that required to give rise to the corresponding line upon the lower half—a fact which is quite unintelligible upon the theory of a central attraction.

Thirdly, in Cucullanus, Ascaris dentata, &c., Kölliker has shown that, though nuclei are developed, no yelk-division occurs ; and in the later stages of division of the frog's egg yelk masses are found undivided, and containing many nuclei.

Finally, in Ascaris mystax, according to Dr. Nelson,[1] the embryonic vesicles absolutely revolve in circles during the progress of yelk-division—a phenomenon which seems incompatible with the existence of any mutual attractive reaction between themselves and the vitelline mass.

We see, in short, that the effects of the force supposed to be exerted by the nuclei may take place without them, and, on the other hand, that the nuclei may be present without exerting the peculiar forces which they are supposed to possess ; and finally that even if such forces exist, they must be something very different from all the attractive forces of which we have any conception ; and therefore that the hypothesis of nuclear force is no explanation, but merely a fresh name for the difficulty.

We are as little able to discover any evidence of the existence of metabolic forces in the nuclei. The metabolic changes of the tissues—such as we see, for instance, in the conversion of cartilage into bone, of cartilage into connective tissue—do not take place, either primarily or with greater intensity, in the neighbourhood of the nuclei ; a fact of which striking evidence is afforded by ossifying cartilage, in which the first deposit of calcareous matter occurs, not in areæ surrounding each nucleus, as we should expect if they exerted a metabolic influence, but in straight lines, which stretch from the ossified surface into the substance of the matrix of the cartilage, and the amount of calcareous matter in which gradually diminishes as we recede from the ossified part, without the least reference to the nuclei. It is the same with the metamorphosis of the periplast of cartilage when it passes into tendon.

From all this we consider it to be satisfactorily shown, that there is no evidence that the " cells " of living bodies are, in any respect, centres

[1] Philosophical Transactions, 1852.

of those properties, which are called vital forces. What, then, are these cells? it may be asked;—what is the meaning of the unquestionable fact that the first indication of vitality, in the higher organisms at any rate, is the assumption of the cellular structure?

In answering these questions, we would first draw attention to the definition of the nature of development in general, first clearly enunciated by Von Baer. "The history of development," he says, "is the history of a gradually increasing differentiation of that which was at first homogeneous." The yelk is homogeneous; the blastoderma is a portion of it which becomes different from the rest, as the result of the operation of the laws of growth; the blastoderma, again, comparatively homogeneous, becomes differentiated into two or more layers; the layers, originally identical throughout, set up different actions in their various parts, and are differentiated into dorsal and visceral plates, chorda dorsalis and bodies of vertebræ, &c., &c. No one, however, imagines that there is any causal connexion between these successive morphological states. No one has dreamt of explaining the development of the dorsal and visceral plates by blastodermic force, nor that of the vertebræ by chorda-dorsalic force. On the other hand, all these states are considered, and justly, to result from the operation of some common determining power, apart from them all—to be, in fact, the modes of manifestation of that power.

Now, why should we not extend this view to histology, which, as we have explained, is only ultimate morphology? As the whole animal is the result of the differentiation of a structureless yelk, so is every tissue the result of the differentiation of a structureless blastema—the first step in that differentiation being the separation of the blastema into endoplast and periplast, or the formation of what is called a "nucleated cell." [1] Then, just as in the development of the embryo, when the blastodermic membrane is once formed, new organs are not developed in other parts of the yelk, but proceed wholly from the differentiation of the blastoderm,—so histologically, the "nucleated cell," the periplast with its endoplast, once formed, further development takes place by their growth and differentiation into new endoplasts and periplasts. The further change into a special tissue, of course, succeeds and results from this primary differentiation, as we have seen the bodies of the vertebræ succeed the chorda dorsalis; but is there any more reason for supposing a causal connexion between the one pair of phenomena than between the other? The cellular structure precedes the special structure; but is the latter, therefore, the result of

[1] Compare Reichert, p. 35.

a "cell-force," of whose existence there is on other grounds no evidence whatever? We must answer in the negative. For us the primarily cellular structure of plants and animals is simply a fact in the history of their histological development—a histologically necessary stage, if one may so call it, which has no more causal connexion with that which follows it, than the equally puzzling morphological necessity for the existence of a chorda dorsalis or of Wolffian bodies has with the development of the true vertebræ or of the true kidneys.

If this be true, we might expect, as we find, that the differentiation of the germinal disc, for instance, into a primitive groove and lateral portions—the first stage of development in the embryo of all vetebrate animals—does not occur in mollusks; as we find, again, that the differentiation of the embryo into plumula and cotyledons which occurs in a great number of plants is absent in others; so if, like these, the histological differentiation into cells have no necessary causal connexion with the action of the vital forces, but be merely a genetic state, we may expect to meet with cases in which it does not occur. Such, in fact, are the so-called unicellular plants and animals—organisms which often exhibit no small complexity of external form, but present no internal histological differentiation. In the genus Caulerpa we have an Alga presenting apparent leaves, stems, and roots, and yet which, according to Nägeli, consists of a single cell—that is, is not composed of cells at all. The Vorticellæ furnish us with examples of animals provided with a distinct œsophagus, a muscular pedicle, &c., and yet in which no further histological differentiation can be made out. As Wolff[1] says—

"The latter (Roesel's Proteus) has no structure, no determinate figure, and even the indeterminate figure that it has at any given time does not remain the same, but alters continually. We can, in fact, regard all these plants and animals as little else than living or vegetating matters—hardly as organized bodies.

"§ 74. However, all these plants and animals nourish themselves, vegetate, and propagate their species, just as well and as easily as the most artificial pieces of mechanism to be met with in the vegetable or animal kingdom."

It is true, indeed, that the difficulty with regard to these organisms has been evaded by calling them "unicellular"—by supposing them to be merely enlarged and modified simple cells; but does not the phrase an "unicellular organism" involve a contradiction for the cell-theory? In the terms of the cell-theory, is not the cell supposed to be an

[1] 'Von der wesentlichen Kraft,' p. 40.

anatomical and physiological unity, capable of performing one function only—the life of the organism being the life of the separate cells of which it is composed? and is not a cell with different organs and functions something totally different from what we mean by a cell among the higher animals? We must say that the admission of the existence of unicellular organisms appears to us to be virtually giving up the cell-theory for these organisms. If it be once admitted that a particle of vitalizable matter may assume a definite and complex form, may take on different functions in its different parts, and may exhibit all the phenomena of life, without assuming the cellular structure, we think that it necessarily follows that the cells are not the centres of the manifestation of the vital forces; or that, if they be so, the nature of these forces is different in the lower organisms from what it is in the higher—a proposition which probably few would feel disposed to maintain.

So much for the critical, and therefore more or less ungrateful, portion of our task. We have seen how the great idea, fully possessed by Fallopius, that life is not the effect of organization, nor necessarily dependent upon it, but, on the other hand, that organization is only one of the phenomena presented by living matter—carried to absurdity by Stahl and Van Helmont—has, on the other hand, been too much neglected by the later writers who have attempted to reduce life to the mere attractions and repulsions of organic centres, or to consider physiology simply as a complex branch of mere physics. We have seen how this latter notion has been fostered by the misconceptions of a great botanist, only too faithfully followed in the animal world by the illustrious author of the cell-theory; and we have endeavoured to show how the solitary genius of Wolff had kept in the old track, and that the choice of modern histologists lies between him and Schleiden and Schwann. It will be sufficiently obvious that our own election has long been made in this matter, and we beg to submit the following sketch of a general theory of the structure of plants and animals—conceived in the spirit, and not unfrequently borrowing the phraseology, of Wolff and Von Baer.

Vitality, the faculty, that is, of exhibiting definite cycles of change in form and composition, is a property inherent in certain kinds of matter.

There is a condition of all kinds of living matter in which it is an amorphous germ—that is, in which its external form depends merely on ordinary physical laws, and in which it possesses no internal structure.

Now, according to the nature of certain previous conditions—the

character of the changes undergone—of the different states necessarily exhibited—or, in other words, the successive differentiations of the amorphous mass will be different.

Conceived as a whole, from their commencement to their termination, they constitute the individuality of the living being, and the passage of the living being through these states is called its development. Development, therefore, and life are, strictly speaking, one thing, though we are accustomed to limit the former to the progressive half of life merely, and to speak of the retrogressive half as decay, considering an imaginary resting point between the two as the adult or perfect state.[1]

The individuality of a living thing, then, or a single life, is a continuous development, and development is the continual differentiation, the constant cyclical change of that which was, at first, morphologically and chemically indifferent and homogeneous.

The morphological differentiation may be of two kinds. In the lowest animals and plants—the so-called unicellular organisms—it may be said to be *external*, the changes of form being essentially confined to the outward shape of the germ, and being unaccompanied by the development of any internal structure.

But in all other animals and plants, an internal morphological differentiation precedes or accompanies the external, and the homogeneous germ becomes separated into a certain central portion, which we have called the *endoplast*, and a peripheral portion, the *periplast*. Inasmuch as the separate existence of the former necessarily implies a cavity, in which it lies, the germ in this state constitutes a vesicle with a central particle, or a "nucleated cell."

There is no evidence whatever that the molecular forces of the living matter (the "vis essentialis" of Wolff, or the vital forces of the moderns) are by this act of differentiation localized in the endoplast, to the exclusion of the periplast, or *vice versa*. Neither is there any evidence that any attraction or other influence is exercised by the one over the other; the changes which each subsequently undergoes, though they are in harmony, having no causal connexion with one another, but each proceeding, as it would seem, in accordance with the general determining laws of the organism. On the other hand, the "vis essentialis" appears to have essentially different and independent ends in view—if we may for the nonce speak metaphorically—in thus separating the endoplast from the periplast.

[1] Dr. Lyons, in his interesting 'Researches on the Primary Stages of Histogenesis and Histolysis,' has invented a most convenient and appropriate term for this latter half of development, so far as the tissues are concerned—viz., Histolysis.

The endoplast grows and divides; but, except in a few more or less doubtful cases, it would seem to undergo no other morphological change. It frequently disappears altogether; but, as a rule, it undergoes neither chemical nor morphological metamorphosis. So far from being the centre of activity of the vital actions, it would appear much rather to be the less important histological element.

The periplast, on the other hand, which has hitherto passed under the names of cell-wall, contents, and intercellular substance, is the subject of all the most important metamorphic processes, whether morphological or chemical, in the animal and in the plant. By its differentiation, every variety of tissue is produced; and this differentiation is the result not of any metabolic action of the endoplast, which has frequently disappeared before the metamorphosis begins, but of intimate molecular changes in its substance, which take place under the guidance of the "vis essentialis," or, to use a strictly positive phrase, occur in a definite order, we know not why.

The metamorphoses of the periplastic substance are twofold—chemical and structural. The former may be of the nature either of *conversion:* change of cellulose into xylogen, intercellular substance, &c., of the indifferent tissue of embryos into collagen, chondrin, &c.; or of *deposit:* as of silica in plants, of calcareous salts in animals.

The structural metamorphoses, again, are of two kinds—*vacuolation*, or the formation of cavities; as in the intercellular passages of plants, the first vascular canals of animals; and *fibrillation*, or the development of a tendency to break up in certain definite lines rather than in others, a peculiar modification of the cohesive forces of the tissue, such as we have in connective tissue, in muscle, and in the "secondary deposits" of the vegetable cell.

Now to illustrate and explain these views, let us return to the vegetable and animal tissues, as we left them in describing the base of the Sphagnum leaf and fœtal cartilage, and trace out the modification of these, which are identical with all young tissues, into some of the typical adult forms.

The point of the Sphagnum leaf is older than the base, and it is easy to trace every stage from the youngest to the complete forms in this direction. At the base of the leaf we find, as has been said, nothing but minute endoplasts, each resembling the other, embedded in a homogeneous periplastic substance (A); as we trace these upwards, we find that some of the endoplasts increase in size more rapidly than the others (B), and eventually *totally disappear*, leaving only the endoplastic cavity, or "cell," which contained them. In the surrounding cells, the endoplasts are very obvious as granular primordial utricles

(C). After the disappearance of the endoplast, changes commence in the periplastic substance or wall of the cell (*a*), more or less circular or spiral thickenings (*c*) taking place in it, so as to form the well-known fibre-cell of the sphagnum leaf; and at the same time, a process of resorption occurs in particular parts of the wall, so that round apertures are formed (*d*). Nothing can be more instructive than this case, the leaf being composed of a single layer of delicate and transparent cells, so that there are no interfering difficulties of observation; and we see demonstrated, in the most striking manner, that the endoplast or primordial utricle has nothing to do with the metamorphoses which occur in the periplastic substance. The disappearance of the primordial utricle in cells which are undergoing thickening was, in truth, long ago pointed out by Von Mohl; but neither he nor any of his successors seem to have noticed how completely this fact does away with that activity of the primordial utricle, and passivity of the cell-wall, which they all assume. We have here, in fact, the cell-wall commencing and carrying through its morphological changes after the primordial utricle has completely disappeared, and we see that the so-called secondary deposit in this case is a morphological differentiation of the periplast, which at the same time exhibits its peculiar powers by setting up a resorption of its substance at another point. Here however, we have no marked chemical differentiation; for an instance of which we may turn to the collenchyma of the beet-root (fig. 1, A.) There is no question that, at one period of its development, the whole periplastic substance here, as in the Sphagnum, was homogeneous, and of the same chemical constitution. In the fully formed beet-root, however, we have no less than three compounds disposed around each cell cavity. The periplastic substance has, in fact, undergone both a chemical and a morphological differentiation—the innermost layers (*c*) consisting of ordinary cellulose;

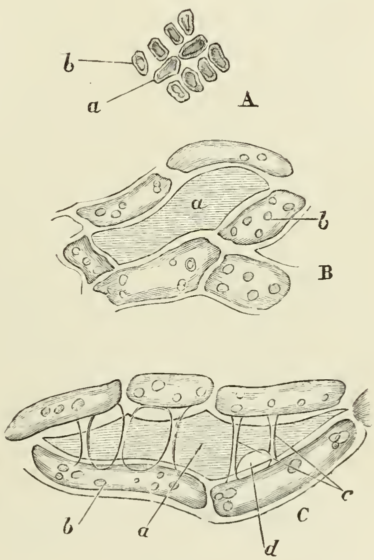


FIG. 2.

Portions of the leaf of Sphagnum. A, from the base; B, more towards the point; C, fully formed. *a*, endoplasts which disappear; *b*, those which remain; *c*, spiral thickenings of periplast in the cavities of the former; *d*, apertures formed by resorption.

the next of a substance which swells up in water (*b*); and the outermost of a different, but not exactly defined, substance (*a*). We may call one of these portions "cell-membrane," and another intercellular substance, but they are assuredly all nothing but differentiated portions of one and the same periplast.

Woody tissue presents precisely the same phenomena, the inner layers of the periplastic substance having, very generally, a different composition from the outer.

Morphologically, we have already noticed the lamination of the periplastic substance, and we may mention its fibrillation, a process which takes place almost invariably in the inner layers of the periplast, and to which the well-known spirality of the so-called secondary deposits must be referred; but a more important process for our; present purpose is what we have called Vacuolation; the development of cavities in the periplastic substance independent of the endoplast, and which, to distinguish them from the cells, may conveniently be termed *Vacuolæ*. In the youngest vegetable tissues there are no such cavities, the periplastic substance forming a continuous solid whole; and it is by this vacuolation, which occurs as the part grows older, that all the intercellular passages are formed, and that many cells obtain that spurious anatomical independence to which we have adverted above. The exaggerated development of the vacuolæ in the pith of the rush converts the periplastic substance, with its proper endoplastic cavities, into regular stellate cells. (Fig. 1, B.)

Sufficient has been said to illustrate the differentiation of the primitive vegetable structure into its most complex forms. If we turn to the animal tissues, we shall find the same simple principles amply sufficient to account for all their varieties.

In the plant, as we have seen, there are but two histological elements—the periplastic substance and the endoplasts, cell-wall and intercellular substance, being merely names for differentiated portions of the former; cell-contents, on the other hand, representing a part of the latter. In the animal, on the other hand, if we are to put faith in the present nomenclature, we find cell-wall, intercellular substance, and cell-contents, forming primitive elements of the tissues, and entering into their composition as such: there have been no small disputes whether the collagenous portion of connective tissue is intercellular substance or cell-wall, the elastic element being pretty generally admitted to be developed from distinct cells. Again, it appears to be usual to consider the fibrillæ of striped muscle as modified cell-contents, while the sarcolemma represents the cell-walls. The hyaline substance of cartilage is asserted by some to be cell-wall, by some to

be intercellular substance; while the walls of the epithelium cavities are admitted on all hands to be cell-walls. We confess ourselves quite unable to find any guiding principle for this nomenclature, unless it be that the toughest structure surrounding a "nucleus" is to be taken as cell-wall, anything soft inside it being contents, and anything external to it intercellular substance; which is hardly a caricature of the vagueness which pervades histological works upon this subject. This results, we think, from the attempt to determine the homology of the parts of the tissues having been made from the examination of their embryonic conditions, where it is often very obscure, and hardly to be made out. It is another matter if we adopt the "principle of continuity" of Reichert—a method of investigation which has been much neglected. This principle is simply, that whatever histological elements pass into one another by insensible gradations are homologous and of the same nature; and it is so clear and easy of application, that we can but wonder at its hitherto limited use. We will now proceed to analyze the nature of the constituents of some of the most characteristic tissues in this way, starting from that of embryonic cartilage, as we have described it above.

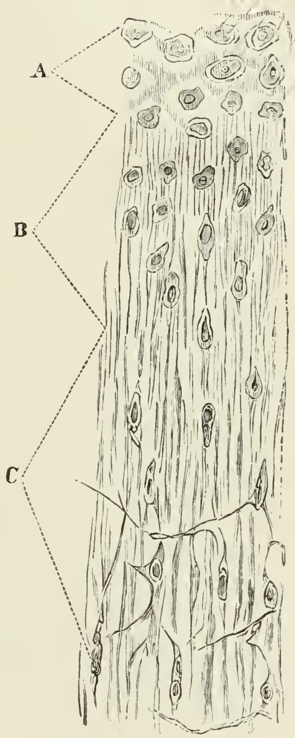


FIG. 3.

Junction of tendo-Achillis and cartilage of the calcaneum in a kitten. A, Pure cartilage; B, intermediate portion; C, tendon. It must be understood that the transition is in reality much more gradual, the different stages having here been approximated for the sake of economizing space.

Connective tissue occurs in two forms,—which, however, pass into one another by infinite gradations,—the solid and the areolated: of the former we may take a tendon as an example; of the latter, the loose areolar tissue, which is found forming the inner layer of the skin and mucous membranes. Fig. 3 represents the junction between the tendo-Achillis and the cartilage of the os calcis in a young kitten. At A we have pure cartilage, the endoplasts lying within cavities whose walls present more or less defined contours. At B, the cavities and their contained endoplasts are somewhat elongated, and a faint striation is obvious in the upper portion of the periplastic substance, which

becomes stronger and stronger as we proceed lower down, until it ends in an apparent fibrillation. A chemical change has at the same time taken place, so that in this portion the striated part of the periplast is swollen up more or less by acetic acid, the walls of the cavities remaining unaffected, and thence becoming more distinct; while in the portion A, the whole periplast was nearly equally insensible to this re-agent. The portion C, nearest the tendon, and passing into it, is completely tendinous in its structure. The periplast exhibits strong fibrillation, and is very sensitive to acetic acid, while not only the walls of the cavities, but the intermediate periplast, in certain directions, which radiate irregularly from them, have changed into a substance which resists acetic acid even more than before, and is in fact elastic tissue. Compare this process with that which we have seen to be undergone by the collenchyma of the beetroot, and we have the fibrillation of the outer portion of the periplast around each endoplast, and its conversion into collagen, answering to the lamination of the "intercellular substance," and its conversion into a vegetable gelatinous matter, while the elastic corresponds with the cellulose inner wall.

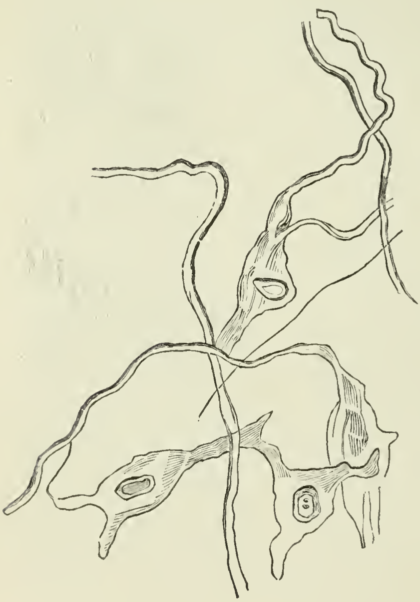


Fig. 4.

Stellate "cells" of young connective tissue from the actinenchyma of the enamel organ of the calf.

The testimony of numerous observers agrees that cartilage is converted into connective tissue in the way described. Professor Kölliker, who unwillingly admits the fact, suggests, nevertheless, that such connective tissue as this is not true connective tissue, inasmuch as it presents differences in its mode of development, the collagenous element in the latter being always developed from cells.[1]

Now, we might be inclined to ask, if the substance of the tendo-Achillis is *not* connective tissue, but only "*täuschend ähnlich*," what is? But it is better to attack Prof. Kölliker's stronghold, the areolated

[1] Handbuch, pp. 58, 59, 218.

gelatinous connective tissue, which is, as he justly observes, the early form of fœtal connective tissue generally. (l. c., p. 58.) If the outer layer of the corium of the skin, or the submucous gelatinous tissue in the enamel organ, be teased out with needles, we shall obtain various stellate or ramified bodies containing endoplasts (fig. 4), which Kölliker calls cells, and which, as he states, do assuredly pass into and become bundles of fibrillated connective tissue. But is this really a different mode of development from that already described? We think not. Indeed, if that portion of this young gelatinous connective tissue, which lies immediately adjacent to the epidermis or epithelium, be examined, it will be found to present a structure in all respects similar to fœtal cartilage, that is, there is a homogeneous matrix in which the endoplasts are dispersed (fig. 5, B). If this be traced inwards, it will be found that the endoplasts become more widely separated from one another, and that the matrix in places between them is softened and altered, while in their immediate neighbourhood, and in the direction of irregular lines stretching from them, it is unaltered. This is, in fact, the first stage of that process which we have called vacuolation. In this condition the intermediate softened spots still retain sufficient consistence not to flow out of a section; but yielding, as it does, in these localities, much more readily than in others, it is easy enough to tear out the firmer portion in the shape of "cells," which are fusiform, irregular, or stellate; and the whole tissue has therefore been described (Reichert, Virchow, Schwann) as consisting of cells connected by an "intercellular substance." Both "cell-walls" and "intercellular substance," however, are portions of the same periplast, and together correspond with the matrix of the cartilage. When, therefore, in the course of further development, the "intercellular substance" becomes quite fluid and so disappears, the outer portion of these cells being converted into fibrillated collagenous tissue, and the inner into elastic substance, we have, notwithstanding the apparently great difference

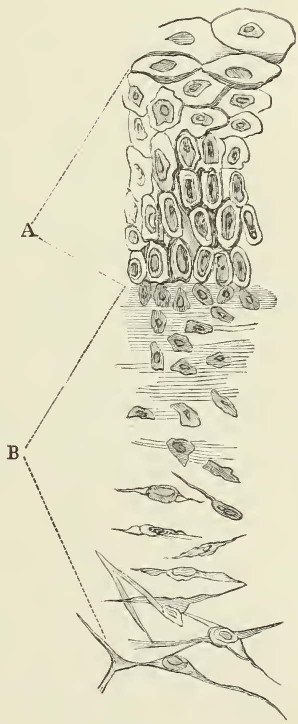


Fig. 5.

Submucous tissue and epithelium of the tongue of the kitten. A, Epithelium; B, young connective tissue.

in reality exactly the same mode of metamorphosis of the same elements as in the preceding instance. Connective tissue, therefore, we may say, consists in its earliest state of a homogeneous periplast inclosing endoplasts. The endoplasts may elongate to some extent, but eventually become lost, and cease, more or less completely, to be distinguishable elements of the tissue. The periplast may undergo three distinct varieties of chemical differentiation, e.g., into the gelatinous "intercellular substance," the collagenous "cell-wall," and the elastic "cell-wall;" and two varieties of morphological differentiation, vacuolation, and fibrillation—and the mode in which these changes take place gives rise to the notion that the perfect tissue is composed of elements chemically and mechanically distinct.

The proper understanding of the nature and mode of development of the component parts of connective tissue is, we believe, of the first importance in comprehending the other tissues. If we clearly bear in mind, in the first place, that the periplast is capable of undergoing modifications quite independently of the endoplasts; and, secondly, that in consequence of their modification, elements may become optically, mechanically, or chemically separable from a perfect tissue which were not discoverable in its young form, and never had any separate existence; many of the great difficulties and perplexities of the cell-theory will disappear. Thus, for instance, with regard to the structure of bone, there can be no doubt that the "nuclei" of the corpuscles are endoplasts, and that the calcified matrix is the periplast. This calcified matrix has, however, in adult bone, very often a very regular structure, being composed of definite particles. To account for these, Messrs. Tomes and De Morgan, in their valuable essay on ossification, which has just appeared,[1] suppose that certain "osteal cells" exist and become ossified. We have no intention here of entering upon the question of the existence of these "osteal cells" as a matter of fact, but we may remark that they are by no means necessary, as the appearance might arise from a differentiation of the periplast into definite particles, corresponding with that which gives to connective tissue its definite and fibrillated aspect. So with regard to the vexed question whether the lacunæ have separate parietes or not, how readily comprehensible the opposite results at which different observers have arrived become, if we consider that their demonstrability or otherwise results simply from the nature and amount of the chemical difference which has been established in the periplast in the immediate neighbourhood of the endoplast with regard to that in the rest of the periplast. In fig. 3 substitute calcific for collagenous metamorphosis,

[1] Phil. Trans., 1853.

and we should have a piece of bone exhibiting every variety of lacunæ, from those without distinct walls to those which constitute regular stellate "bone corpuscles." Finally, in bone, the formation of the "Haversian spaces" of Tomes and De Morgan is a process of vacuolation, strictly comparable to that which we have described as giving rise to the areolated connective tissue. Cancellated bone is, in fact, areolated osseous tissue. Once having comprehended the fact that the periplast is the metamorphic element of the tissues, and that the endoplast has no influence nor importance in histological metamorphosis, there ceases to be any difficulty in understanding and admitting the development of the tubules of the dentine and the prisms of the enamel, without the intervention of endoplasts. These are but extreme and obvious cases in which nature has separated for us two histological elements and two processes, which are elsewhere confounded together.

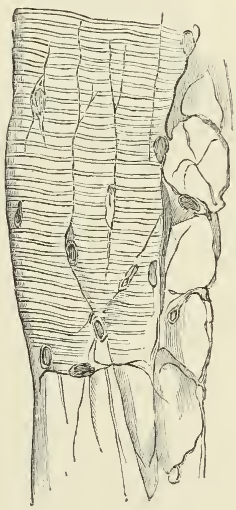


FIG. 6.

Continuity of muscle with connective tissue from the tongue of the lamb. A, Connective tissue; B, muscle.

One of the most complicated of tissues is striped muscle, yet the true homology of its elements seems to us to become intelligible enough upon these principles. Dr. Hyde Salter has pointed out,[1] that in the tongue the muscles pass directly into the bundles of the submucous connective tissue which serve as their tendons. We have figured such a transition in fig. 6. The tendon A may be seen passing insensibly into the muscle B, the granular sarcous elements of the latter appearing as it were to be deposited in the substance of the tendon (just as the calcareous particles are deposited in bone), at first leaving the tissue about the walls of the cavities of the endoplasts, and that in some other directions unaltered. These portions, which would have represented the elastic element in ordinary connective tissue, disappear in the centre of the muscular bundle, and the endoplasts are immediately surrounded by muscle, just as, in many specimens of bone, the lacunæ have no distinguishable walls. On the other hand, at the surface of the bundle the representative of the elastic element remains, and often becomes much developed as the sarcolemma. There is no question here of muscle resulting from the

[1] Art. 'Tongue,' Todd's Cyclopædia.

contents of fused cells, &c. It is obviously and readily seen to be nothing but a metamorphosis of the periplastic substance, in all respects comparable to that which occurs in ossification, or in the development of tendon. In this case we might expect that as there is an areolar form of connective tissue, so we should find some similar arrangement of muscle; and such may indeed be seen very beautifully in the terminations of the branched muscles, as they are called. In fig. 7 the termination of such a muscle, from the lip of the rat, is shown, and the stellate "cells" of areolated connective tissue are seen passing into the divided extremities of the muscular bundle, becoming gradually striated as they do so.

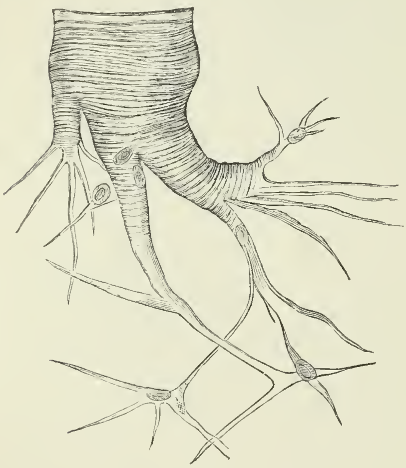


Fig. 7.

Branched muscle, ending in stellate connective "cells," from the upper lip of the rat.

We have already exceeded our due limits, and we must therefore reserve for another place the application of these views to other tissues. There is, however, one application of the mode of termination of the branched muscles to which we have just referred, which is of too great physiological importance to be passed over in silence. In the muscle it is obvious enough that whatever *homology* there may be between the stellate "cells" and the muscular bundles with which they are continuous, there is no *functional analogy*, the stellate bodies having no contractile faculty. But a nervous tubule is developed in essentially the same manner as a muscular fasciculus, the only difference being that fatty matters take the place of syntonin. Now, it commonly happens that the nerve-tubules terminate in stellate bodies of a precisely similar nature; and these, in this case, are supposed to possess important nervous functions, and go by the name of "ganglionic cells." From what has been said, however, it is clear that these may be genetically and not functionally connected with the nervous tubules, and that, so far from being *the* essential element of the nervous centres and expansions, it is possible that the "ganglionic cells" have as little nervous function as the stellate cells in the lip of the rat have contractile function.

We cannot conclude better than by concisely repeating the points to which we have attempted to draw attention in the course of the present article.

We have endeavoured to show that life, so far as it is manifested by structure, is for us nothing but a succession of certain morphological and chemical phenomena in a definite cycle, of whose cause or causes we know nothing; and that, in virtue of their invariable passage through these successive states, living beings have a development, a knowledge of which is necessary to any complete understanding of them. It has been seen that Von Baer enunciated the law of this development, so far as the organs are concerned; that it is a continually increasing differentiation of that which was at first homogeneous; and that Caspar Friedrich Wolff demonstrated the nature of histological development to be essentially the same, though he erred in some points of detail. We have found Schwann demonstrating for the animal, what was already known for the plant—that the first histological differentiation, in the embryo, is into endoplast and periplast, or, in his own phrase, into a "nucleated cell;" and we have endeavoured to show in what way he was misled into a fundamentally erroneous conception of the homologies of these two primitive constituents in plants and animals—that what he calls the "nucleus" in the animal is not the homologue of the "nucleus" in the plant, but of the primordial utricle.

We have brought forward evidence to the effect that this primary differentiation is not a necessary preliminary to further organization—that the cells are not machines by which alone further development can take place, nor, even with Dr. Carpenter's restriction (p. 737), are to be considered as "instrumental" to that development. We have tried to show that they are not instruments, but indications—that they are no more the producers of the vital phenomena than the shells scattered in orderly lines along the sea-beach are the instruments by which the gravitative force of the moon acts upon the ocean. Like these, the cells mark only where the vital tides have been, and how they have acted.

Again, we have failed to discover any satisfactory evidence that the endoplast, once formed, exercises any attractive, metamorphic, or metabolic force upon the periplast; and we have therefore maintained the broad doctrine established by Wolff, that the vital phenomena are not necessarily preceded by organization, nor are in any way the result or effect of formed parts, but that the faculty of manifesting them resides in the matter of which living bodies are composed, as such—

or, to use the language of the day, that the " vital forces " are molecular forces.

It will doubtless be said by many, But what guides these molecular forces? Some Cause, some Force, must rule the atoms and determine their arrangement into cells and organs ; there must be something, call it what you will—Archæus, " Bildungs-trieb," " Vis Essentialis," Vital Force, Cell-force—by whose energy the vital phenomena in each case are what they are.

We have but one answer to such inquiries : Physiology and Ontology are two sciences which cannot be too carefully kept apart ; there may be such entities as causes, powers, and forces, but they are the subjects of the latter, and not of the former science, in which their assumption has hitherto been a mere gaudy cloak for ignorance. For us, physiology is but a branch of the humble philosophy of facts ; and when it has ascertained the phenomena presented by living beings and their order, its powers are exhausted. If cause, power, and force mean anything but convenient names for the mode of association of facts, physiology is powerless to reach them. It is satisfactory to reflect, however, that in this comparatively limited sphere the inquiring mind may yet find much occupation.

XXIV

ON THE VASCULAR SYSTEM OF THE LOWER ANNULOSA

British Association Report 1854 (*Pt.* 2) *p.* 109

UNDER the term Lower Annulosa the author included the Annelida, the Echinodermata, the Trematoda, the Turbellaria, and the Rotifera,—in all of which there exists a peculiar system of vessels which have hitherto been universally regarded as a blood vascular system. Without considering the view he was about to lay before the Section to be fully demonstrated, the author said that he had to offer very strong reasons for regarding the prevalent notion as incorrect. The vascular system of the higher Annulosa and of the Mollusca is in all cases a more or less specialised part of the common cavity of the body. The fluid which it contains is a corpusculated fluid; the propulsive organ, if any special heart exist, is a contractile sac, connected by valvular apertures with that common cavity. Now, although it might be incorrect to say that the vascular system of the lower Annelida is invariably distinguished by characters the opposite of these, still there can be no question that, as a general rule, such is the case; and this circumstance is alone sufficient to raise grave doubts as to the homology of the two systems. But these doubts are greatly strengthened when we take into consideration certain facts, which the author proceeded to lay before the Section. In the Rotifera there is a system of vessels, consisting of a contractile vesicle, opening externally, from which canals, containing long vibratile cilia, pass into the body. In certain Distomata, such as *Aspidogaster conchicola*, there is a system of vessels of essentially similar character; but the principal canals—those lateral trunks which come off directly from the contractile vesicle—present regular rhythmical contractions.

The smaller branches are all richly ciliated. In other Distomata the lateral trunks appear to be converted into excretory organs, as they are full of minute granules ; they remain eminently contractile ; but their connection with the system of smaller ramified vessels ceases to be easy of demonstration. As Van Beneden and others have shown, they still form one system ; but the cilia are no longer to be found in the smaller ramified vessels, having sometimes vanished altogether ; at others, being discoverable only here and there in the minute ultimate terminations of these vessels. In certain Nematoidea the vascular system is reduced to a couple of lateral contractile vessels, altogether devoid of cilia, but communicating, by a small aperture, with the exterior. Now there is no doubt that, in all these cases the "vascular system" is physiologically a respiratory and, perhaps, urinary system ; while the common cavity of the body represents the blood-vascular system of the Mollusca and Articulata. However, Echinorhynchus possesses a vascular system of the same nature as that of a Nematoid or Distomatous worm, but presenting no cilia, and having no external opening ; thus forming a closed vascular system, homologous with those previously described, and differing from them only in the fact of its closure. But from hence it is a very easy and natural transition to the vascular system of the Annelida ; and the author stated his conviction, based not only upon these, but upon many additional reasons, that these so-called blood-vessels, and those of the Echinodermata, form, in fact, only the final term of a series, of which the so-called water-vascular system of the Rotifera constitutes the commencement. If, however, these vessels have really nothing to do with the proper blood-vascular system of the higher Annulosa, with what system of organs are they homologous ? In answer to this question, the author stated his belief that they correspond with the tracheæ of Insecta, which present a similar extensive ramified distribution, and, in some cases, as in the larvæ of the Libellulidæ, constitute as completely closed a system of vessels.

XXV

ON THE COMMON PLAN OF ANIMAL FORMS

Abstract of a Friday Evening Discourse at the Royal Institution, May 12, 1854, *Royal Institute Proceedings, vol. i.*, 1851–4, *pp.* 444–446.]

THE Lecturer commenced by referring to a short essay by Göthe —the last which proceeded from his pen—containing a critical account of a discussion bearing upon the doctrine of the Unity of Organization of Animals, which had then (1830) just taken place in the French Academy. Göthe said that, for him, this controversy was of more importance than the Revolution of July which immediately followed it—a declaration which might almost be regarded as a prophecy; for while the *Charte* and those who established it have vanished as though they had never been, the Doctrine of Unity of Organization retains a profound interest and importance for those who study the science of life.

It would be the object of the Lecturer to explain how the controversy in question arose, and to show what ground of truth was common to the combatants.

The variety of Forms of Animals is best realised, perhaps, by reflecting that there are certainly 200,000 species, and that each species is, in its zoological dignity, not the equivalent of a family or a nation of men merely, but of the whole Human Race. It would be hopeless to attempt to gain a knowledge of these forms, therefore, if it were not possible to discover points of similarity among large numbers of them, and to classify them into groups,—one member of which might be taken to represent the whole. A rough practical classification, based on obvious resemblances, is as old as language itself; and the whole purpose of Zoology and Comparative Anatomy has consisted chiefly in giving greater exactness to the definition and expression of these intuitive perceptions of resemblance.

The Lecturer proceeded to show how the celebrated Camper illustrated these resemblances of the organs of animals, by drawing the arm of a man, and then, by merely altering the proportions of its constituent parts, converting it into a bird's wing, a horse's fore-leg, &c., &c. Organs which can in this way be shown to grade into one another, are said to be the same organs, or in anatomical phraseology are *Homologous*:—and by thus working out the homologies of all the organs of the Vertebrate class, Geoffroy, Oken, and Owen,—to the last of whom we are indebted for by far the most elaborate and logical development of the doctrine,—have demonstrated the homology of all the parts of the Vertebrata, or in other words, that there is a common plan on which all those animals which possess back-bones are constructed.

Precisely the same result has been arrived at, by the same methods, in another great division of the Animal Kingdom—the *Annulosa*. As an illustration, the Lecturer showed how the parts of the mouth of all insects were modifications of the same elements, and briefly sketched the common plan of the Annulosa, as it may be deduced from the investigations of Savigny, Audouin, Milne-Edwards, and Newport.

Leaving out of consideration (for want of time merely) the *Radiate* animals, and passing to the remaining great division, the *Mollusca*,—it appears that the same great principle holds good even for these apparently unsymmetrical and irregular creatures: and the Lecturer, after referring to the demonstration of the common plan upon which those Mollusks possessing heads are constructed,—which he had already given in the Philosophical Transactions,—stated that he was now able to extend that plan to the remaining orders, and briefly explained in what way the 'Archetypal Mollusk' is modified in the *Lamellibranchs*, *Brachiopoda*, *Tunicata*, and *Polyzoa*.

We have then a common plan of the *Vertebrata*, of the *Articulata*, of the *Mollusca*, and of the *Radiata*,—and to come to the essence of the controversy in the Académie des Sciences—are all these common plans identical, or are they not?

Now if we confine ourselves to the sole method which Cuvier admitted—the method of the insensible gradation of forms—there can be no doubt that the Vertebrate, Annulose, and Molluscan plans are sharply and distinctly marked off from one another by very definite characters; and the existence of any common plan, of which they are modifications, is a purely hypothetical assumption, and may or may not be true. But is there any other method of ascertaining a community of plan beside the method of Gradation?

The Lecturer here drew an illustration from Philology—a science which in determining the affinities of words also employs the method of gradation. Thus *unus*, *uno*, *un*, *one*, *ein*, are said to be modifications of the same word, because they pass gradually into one another. So *Hemp*, *Hennep*, *Hanf*, and *Cannabis*, *Canapa*, *Chanvre*, are respectively modifications of the same word ; but suppose we wish to make out what, if any, affinity exists between *Hemp* and *Cannabis*—the method of gradation fails us. It is only by all sorts of arbitrary suppositions that one can be made to pass into the other.

Nevertheless modern Philology demonstrates that the words are the same, by a reference to the independently ascertained laws of change and substitution for the letters of corresponding words, in the Indo-Germanic tongues : by showing in fact, that though these words are not the same, yet they are modifications by known developmental laws of the same root.

Now Von Bär has shown us that the study of development has a precisely similar bearing upon the question of the unity of organization of animals. He indicated, in his masterly essays published five-and-twenty years ago, that though the common plans of the adult forms of the great classes are not identical, yet they start in the course of their development from the same point. And the whole tendency of modern research is to confirm his conclusion.

If then, with the advantage of the great lapse of time and progress of knowledge, we may presume to pronounce judgment where Cuvier and Geoffroy St. Hilaire were the litigants—it may be said that Geoffroy's inspiration was true, but his mode of working it out false. An insect is not a vertebrate animal, nor are its legs free ribs. A cuttlefish is not a vertebrate animal doubled up. But there was a period in the development of each when insect, cuttlefish, and vertebrate were undistinguishable and had a *Common Plan*.

The Lecturer concluded by remarking that the existence of hotly controverted questions between men of knowledge, ability, and especially of honesty and earnestness of purpose, such as Cuvier and his rival were, is an opprobrium to the science which they profess. He would feel deeply rewarded if he had produced in the minds of his hearers the conviction that these two great men—friends as they were to one another—need not be set in scientific opposition ; that they were both true knights doing battle for science ; but that, as the old story runs, each came by his own road to a different side of the shield.

XXVI

ON THE STRUCTURE AND RELATION OF THE CORPUSCULA TACTUS (TACTILE CORPUSCLES OR AXILE CORPUSCLES), AND OF THE PACINIAN BODIES.

Quarterly Journ. Microsc. Sci., vol. ii., 1854, *p.* 1–7.

In February, 1852, Professor Wagner published in the Göttingen 'Gelehrte Nachrichten,' the results of some observations, made by G. Meissner and himself, the tendency of which was to establish the existence of peculiar bodies in certain of the papillæ of the fingers and palm of the hand, to which, from their relation to the nerves entering the papilla, he ascribed special functions, and thence proposed to confer upon them the name of *corpuscula tactus*—Tactile corpuscles. Wagner's principal positions are the following :—

1. The papillæ of the hand are of two kinds—nervous and vascular—the vascular papillæ containing no nerves, and the nervous papillæ possessing no vessels.

2. The nervous papillæ contain a peculiarly constructed oval mass, like a fir-cone, composed of bands or rows, arranged one behind the other.

3. The dark-bordered nerve-fibres enter the papilla, pass to this "tactile corpuscle," and terminate in it, either free or dividing into five branches.

4. These corpuscles are analogous to the Pacinian bodies.

5. They are specially subservient to sensation.

Professor Kölliker, whom this Memoir touched somewhat directly, replied in the 'Zeitschrift für Wissenschaftliche Zoologie' of the following June, by an essay on the same subject (Ueber den Bau der Cutispapillen und der sogenannten Tactkörperche R. Wagner's), in

which, having carefully repeated and extended Wagner's observations, his general conclusions are :—

1. *a.* The corpusculated papillæ often contain vessels.

b. The vascular papillæ of the lip contain nerves.

c. In the lip and hand there are a few papillæ without axile corpuscles and with nerves.

2. The tactile corpuscle is not a peculiar body, but the ordinary embryonic connective tissue remaining as the axis of the papilla. Kölliker therefore proposes to call it " axile corpuscle."

3. The nerves do not enter and terminate in the corpuscle but wind round it and form loops.

4. The corpuscles are not specially subservient to sensation.

Besides the surface of the hand Kölliker found these corpuscles only in the red edges of the lips and at the point of the tongue.

Finally, in Müller's Archiv for 1852, Wagner, in a communication accompanied by very good figures (Ueber der Tactkörperchen, *Corpuscula Tactus*, Müll. Arch. H. 4), referring to the discrepancies between Kölliker and himself, considers the question as to the peculiarity of the structure of the corpuscles to be still open ; he denies that the nerve fibres form loops on the axile corpuscles (quoting, in confirmation of his own views, Meissner, Ecker, Brüche, and Günsburg), and, also, that nerves enter any papillæ but those provided with tactile corpuscles. Wagner admits, however, that certain of the papillæ containing axile corpuscles also exhibit vascular loops, but these, according to him, always have nervous tissue at their extremities, and are in fact formed by the coalescence of a nervous and vascular papilla. Without pretending to decide, when two such eminent doctors in physiology disagree, I beg to lay before the reader the following results of my own examination of this matter, accompanied by some figures drawn on a larger scale, and with more attention to detail than those furnished by Wagner or Kölliker. I can best arrange what I have to say in the order of the points in dispute, as given above.

1. In the human finger I have met with corpusculated papillæ containing vascular loops, though rarely (Pl. I. [XXIV.] fig. 2) ; but I have observed no papillæ without corpuscles, to present nerves. That there is not, however, necessarily an inverse relation between the presence of vessels and that of nerves, is shown by the fungiform papillæ of the sides of the base of the tongue in the Frog, in which very evident dark-contoured nerves may be seen terminating in papillæ, without any trace of a tactile corpuscle, and with a large vascular loop (fig. 6).

2. Everything I have seen leads me to believe with Kölliker, that the 'corpuscle' is not histologically, in any respect, a special structure, but merely rudimentary connective tissue (areolated embryonic connective tissue of Kölliker), exactly resembling that which is to be found in the rest of the papilla. This consists in fact of a homogeneous matrix in which endoplasts (nuclei) are embedded, and which, in various directions surrounding and radiating from these, is metamorphosed into a substance more or less resembling elastic fibre. The sole difference from the surrounding substance presented by the corpuscle consists in this, that these elastic bands and filaments are more or less parallel to one another, and perpendicular to the axis of the corpuscle (fig. 1).

In one respect, however, I believe that the corpuscles are peculiar, and something more than the mere, imperfectly formed axis of the papilla. Kölliker has pointed out (*l. c.* p. 67) that the nerve-tubules which enter the papilla are accompanied by a delicate neurilemma, and I believe that the "corpuscles" are its continuation and termination. In structure, the neurilemma which surrounds the more delicate branches of the nerves in the human finger (fig. 7) is identical with the "corpuscles," except that in the former the elastic element is disposed parallel with the nerve fibre, while in the latter it is more or less perpendicular to it. In fact, I believe, that the "corpuscle" is simply the modified extremity of the neurilemma of the nervous tubules which enter the papillæ.

3. With respect to the extremely difficult question of the mode of termination of the nerves, I may state that, without having any reason to urge against the existence of loops (on the contrary, having observed them very distinctly in the cutaneous papillæ of fishes), I have never been able to convince myself of their presence, and frequently when I believed I had such cases before my eyes, the use of a higher power, or the causing the papilla to turn a little, would undeceive me.

On the other hand, it is by no means difficult to obtain the clearest possible evidence of the occurrence of the so-called free ends (figs. 3, 4, 5). The dark-contoured fibres pass, sometimes only a little beyond the proximal extremity of the corpuscle (figs. 4, 5), sometimes quite to its distal end (fig. 3), and here terminate by one or two pointed extremities, which appear to be continuous with the tissue of the corpuscle. I have never been able to obtain any evidence of the entrance of a dark-contoured nerve fibre into a "corpuscle." My belief that the nerves in the corpusculated papillæ of Man do really terminate in this manner, is strengthened by the ease with which this

mode of termination may be demonstrated in the papillæ of the tongue of the Frog, to which reference has been made above (fig. 6). Here four or five coarse nerve-fibres enter the papilla, run to its very extremity, become pointed, abruptly lose their fatty nature, and terminate in the delicate reticulated fibres, which represent the elastic element of the connective tissue of the part.[1]

4. Wagner, as we have seen, compares the corpuscles to the Pacinian bodies, and I think with great justice. The Pacinian bodies are, as is well known, principally found attached to the nerves of the hand and foot in Man, to those of the mesentery in the cat, to the nerves of the extremities of many animals, to those of the skin and beak in birds, and to the intercostal nerves of the Boa constrictor. They are commonly said to be composed of numerous corpuscles of connective tissue, arranged concentrically, and separated by a clear fluid. The innermost contains, besides this fluid, a nervous fibre, which terminates in a free clavate or branched extremity.

In the human hand, however, I have invariably found that this description of their structure is not exactly correct. In fact, I find no interspaces filled with fluid, nor any central cavity. If the body be cut in two, each half remains as hard and uncollapsed as before ; if it be torn, each layer of the "corpuscle" is seen to be united to its neighbour by a delicate, transparent, more or less granular, or sometimes fibrillated substance. Again, the nerve lies not in a cavity, but in a solid homogeneous substance ; and, so far as I have seen, terminates more or less gradually in a portion of this mass, in which great numbers of endoplasts (nuclei) lie, and which has thence almost the appearance of cartilage.[2] The structure of the rest of the body is,

[1] Much has been said as to the possibility of confounding capillaries with nerves ; but I conceive that such a mistake could hardly be made by any careful observer, unless perhaps strong alkaline solutions had been allowed to act unwatched upon the preparation. I have made use of both acetic acid and caustic soda, and I find the latter more available in discovering nerves, the former in making out vessels and the general structure of the papilla ; inasmuch as it renders their "nuclei" more obvious, while soda makes them less so. It is very useful sometimes to use these re-agents alternately ; and it is a good rule to apply them to the object only while under the microscope, so as to watch their gradual operation.

[2] According to Will (Reichert's Report, p. 69, Müll. Arch. 1851), the contents of the central capsule of the Pacinian body in Birds is formed by a dense cellular mass, and closely applied cells exist in the external neurilemma. From observations upon these bodies in the Pigeon and Duck I can confirm this statement : in fact, the Pacinian bodies of the birds are very like the young forms of those of Man. I have also noticed, as Wagner states (l. c. p. 499), that the internal cellular mass is occasionally transversely striated, somewhat like a tactile corpuscle. The Pacinian bodies in Birds are much more superficial than in Man, being situated in the superficial layer of the corium, close to the sacs of the feathers. In the Pigeon they are very small, frequently not more than 1-150th—1-200th of an inch in their

essentially, the same,[1] and the appearance of their concentric capsules is produced by the arrangement of their endoplasts in concentric layers in the outer part of the Pacinian body, and their connexion by the laminæ and fibres of more or less imperfect elastic substance.

The concentric lines in the Pacinian bodies are no more evidence that they are composed of capsules, than the parallel lines in the neurilemma of small nervous twigs (fig. 7) are evidence that it is composed of concentric tubes. In each case the appearances depend simply upon the disposition of the lines of elastic tissue. In fact, the Pacinian bodies are nothing more than thickened processes of the neurilemma of the nerve to which they are attached ; and differ from the "tactile corpuscles" only in the circumstance that the thickening takes place on each side of the nerve fibril, while in the Pacinian body it takes place on both sides. The difference in the direction of the apparent layers is not so great as it seems, since, at each extremity of the Pacinian body, these are, as in the tactile corpuscle, perpendicular to the direction of the nerve.

5. The evidence with respect to the physiological functions of either the *corpuscula tactus* or of the Pacinian bodies is wholly negative ; and it seems useless to enter upon the region of hypothetical suppositions. But I think that Comparative Anatomy promises to offer some assistance in this case by showing that these structures form the lowest terms, in a series whose higher members attain a very great development in certain animals, though their precise function is in many cases obscure. The homology of the tactile corpuscles with the Pacinian bodies appears, from what has been said, to be clear What are the Pacinian bodies? Mr. Bowman, in his article on this subject in the Cyclopædia of Anatomy, will not decide upon their function, but points out their close similarity to certain bodies described by Savi in the Torpedo, and subsequently more fully described by Leydig (Beiträge zur Anat. d. Rochen. u. Haie.). These are capsules of homogeneous connective tissue, containing a semi-solid gelatinous substance, and inclosing a knob-like process ; the termina-

long diameter, and possess only one or two "capsules," with a proportionally large inner mass. In the Duck they are to be met with in great numbers in the skin of the beak, especially in the ridged portion at its edges. Here the Pacinian bodies, often very small (1-400th of an inch), lie immediately under the epidermis, with their long diameters more or less parallel to the surface ; and the nerves are related to them, just in the same manner as those of the fingers are to the tactile corpuscle. It is difficult to suppose that they have not here some special reference to the sense of touch.

[1] Compare Strahl. Müll. Archiv, 1848, who gives a similar account of the structure of the layers.

tion of the stalk of the vesicle. A nervous bundle passes through the stalk, accompanied by a vessel, and branches out in the knob; its fibres become pale and terminate here, not passing through as Savi stated. (Diag. C.)

In the Rays and Sharks, bodies precisely similar to these, open by a tubular neck upon the outer surface of the skin. In the Sharks they have no special external hard capsule, while in the Rays they are provided with such a capsule, composed of condensed connective tissue. (Diag. D. E.)

In the osseous Fishes, ampullæ, similar to these, connected together by a longitudinal tube open on the sides of the body along the so-called lateral line. The systems of each side are connected by a transverse tube which passes over the occiput. In the Sharks and Rays, organs of an exactly similar nature form a system of ramifying tubes in the head and over the sides of the body. These organs have hitherto been known as the "muciparous canals;" though, as Leydig has well shown, they contain a semi-solid gelatinous material, and have nothing to do with the mucus of the skin, which is formed by the altered epidermic layer. As Leydig has pointed out, then—the *Pacinian bodies*, the *Savian bodies*, and the so-called *muciparous canals* of osseous and cartilaginous fishes are homologous organs, and form a series, whose lowest term, if Wagner's conclusion be correct, is formed by the *corpuscula tactus*. What is the highest term? In the most complex ampulla, or muciparous canal, of a Ray or Shark, we find—1. externally a thick coat, composed of condensed connective tissue; 2. a nervous twig penetrating this, and passing to—3. an internal delicate sac, which contains a gelatinous matter, communicates with the exterior, and is lined by a layer of cells continuous with the epidermis: on the walls of this the vessels and nerves terminate. Now, we have only to conceive a single hair, developed within one of these ampullæ and taking the place of the clear gelatinous matter, to have a *vibrissa*, such as is met with in almost all the Mammalia about the lip and eyebrow (see Diagr. F); and I conceive that the *vibrissæ* are, in fact, the most complex and fully developed forms of this series of cutaneous organs.[1] Now, the *vibrissæ* are, without doubt, delicate organs of touch, and the mucous canals of Fishes appear to be very probably of the same nature; but when we come to the Savian and Pacinian bodies, and to the Corpuscula tactus, two

[1] The auditory labyrinth is constructed on precisely the same plan as the muciparous canals of fishes, and the eye on that of a *vibrissa*, as might readily be demonstrated; so that all the organs of sense are to be regarded as modifications of one and the same plan.

possibilities arise—either they may be still the instruments of a modified sense of touch, or they may be merely rudimentary representatives of the more completely formed organs. At present there appears to be no sufficient evidence to decide this point; and I would merely wish to draw attention to the fact, that these organs are not isolated structures, but form a series, with the function of whose highest members only, we are at present fully acquainted.

DESCRIPTION OF PLATE I., Vol. II. [Plate XXIV.]

Fig. 1. Four papillæ from the point of the finger; the largest containing a tactile corpuscle with its nerves, while the others possess capillary loops. Acetic acid added—*a.* Nerves. *b.* Neurilemma. *c.* "Nuclei." *d.* Capillaries.

Fig. 2. A papilla from the finger of a Tahitian, with a small tactile corpuscle. Letters as above. Acetic acid added.

Figs. 3, 4, 5. Termination of nerve-fibres against tactile corpuscles. Caustic soda added. ·600.

Fig. 6. Extremity of one of the papillæ at the base of a Frog's tongue, the epithelium being stripped off.

Fig. 7. A nerve, consisting of a single, dark-contoured fibril in its neurilemma, from the human finger.

Fig. 8. Portion of the wall of a Pacinian body from the human finger.

Fig. 9. Section perpendicularly through one of the ridges on the beak of a Duck. *l.* Horny layer of epidermis. *m.* Mucous layer. *n.* Derma. *p.* Pacinian bodies.

Fig. 10. A single Pacinian body of the same.

Diagrams.

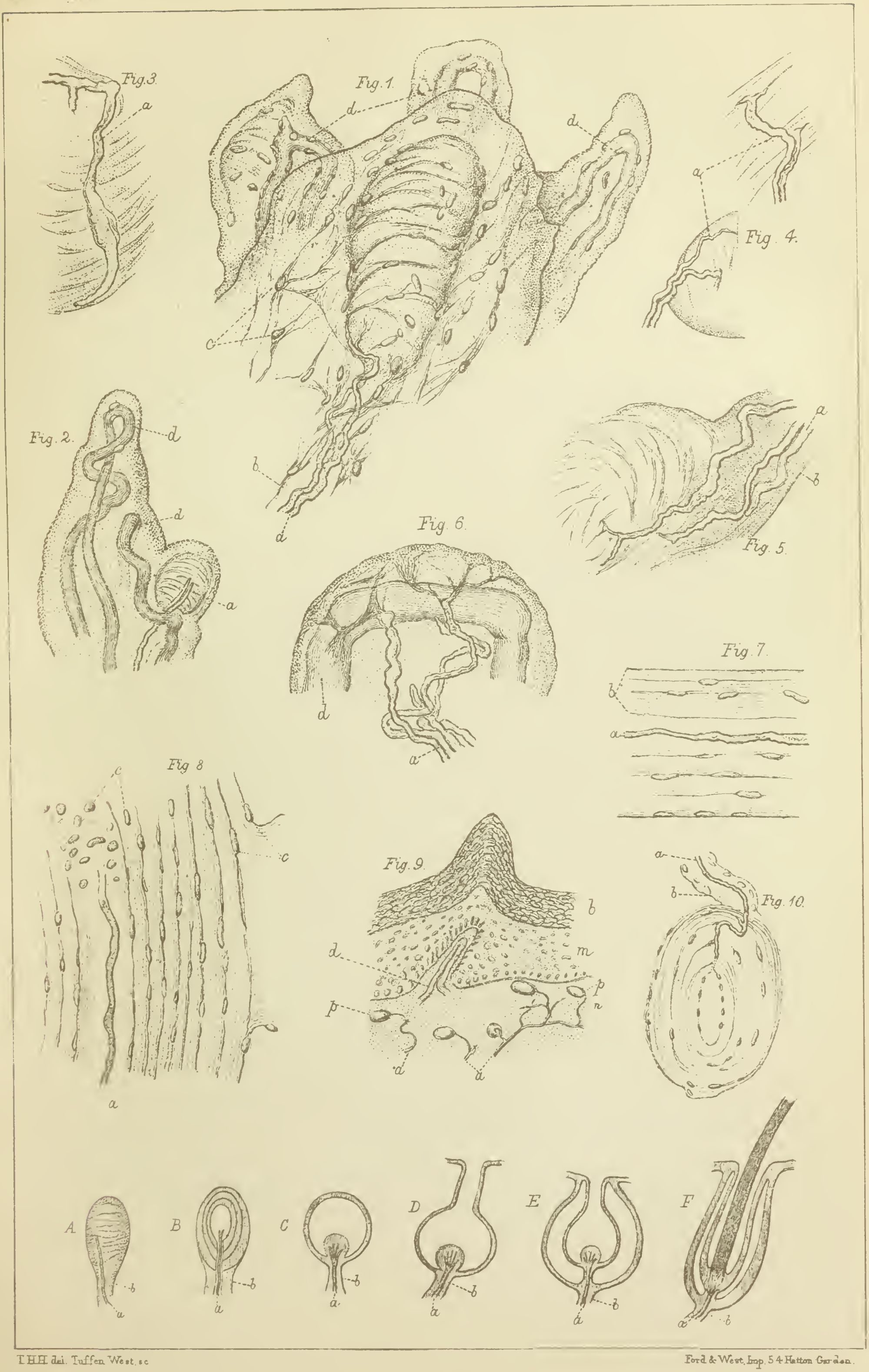
A. Of a Tactile corpuscle.

B. Of a Pacinian body.

C. Of a Savian body.

D. Of the "Muciparous Canals" of fishes.

E. Of a Vibrissa of a rat.



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XXVII

ON THE ULTIMATE STRUCTURE AND RELATIONS OF THE MALPIGHIAN BODIES OF THE SPLEEN AND OF THE TONSILLAR FOLLICLES

Journ. Microsc. Sci., vol. ii., 1854, *pp.* 74–82

THE first account of those peculiar whitish corpuscles, discovered by Malpighi and to be met with, more or less distinctly marked, in the spleen of every animal, which at all satisfies the requirements of modern anatomical science, was given by Professor Müller, in his Archiv. for 1834. Müller describes with great accuracy the mode in which these bodies are supplied by minute arteries, and explains that they are, in fact, outgrowths of the adventitious tunic of those arteries. He states that, by means of fine injections, he found that "the arterial twigs sometimes passed by the side of the Malpighian bodies without giving off any branches to them—sometimes went straight through the whole body or a part of it, in which case, however, no portion of the arteries terminated in them. These fine arterial twigs appear less to pass through the middle of the corpuscles than to run on their walls and then to leave them. When an arterial twig divides into many minute branches in the Malpighian body, which never takes place upon its surface, but always in the thickness of its walls, these arterioles pass out again to be distributed as very minute branches in the surrounding red pulp: in fact, the ultimate termination of all the finest penicellate arteries is in this red substance. From all this I have become convinced that the white bodies, as mere outgrowths of the *tunicæ adventitiæ*, have no relation with the finest ramifications of the arteries."

With regard to another important point,—whether the Malpighian bodies are hollow or solid—Professor Müller's statements are less definite. In the commencement of his article he affirms, in opposition

to Malpighi and Rudolphi, that they are solid, but at the end he qualifies this opinion : "I was long of opinion that the white bodies are not hollow, but merely filled with a white pulpy substance, which might indeed be pressed out of them, but was not distinctly defined from the walls of the bodies. Further observations recently made, however, have instructed me that the white granular substance which is contained in the Malpighian bodies is too fluid, while on the other hand their walls are too solid, not to oblige us to regard them as a kind of vesicles with tolerably thick walls. The white clear fluid (breiige) matter which they contain consists for the most part of equal-sized corpuscles, which are about as large as the blood-corpuscles—not however flat, like these, but irregularly globular. These corpuscles present exactly the same microscopic appearance, and are of the same size, as the granules of which the red substance of the spleen is composed." Pp. 88, 89.

Although the Malpighian bodies have been the subject of frequent and repeated investigations since 1834, I think that more has been done to confuse than to improve the above (in its general outlines) very accurate account of their structure.

Giesker, in a work which I have not seen (Splenologie, 1835, cited by both Henle and Kölliker), appears to have been the first to diverge from Müller's views. He states that there is a delicate membrane investing the proper membranes of the Malpighian bodies in which arterioles ramify—and thus the latter never enter the Malpighian bodies at all (Henle, Allg. Anat. p. 1000) ; and Kölliker, Gerlach, and Sanders (On the Structure of the Spleen, Annals of Anat. and Phys. 1850), agree with Giesker on the latter point.

In the meanwhile, however, Günsburg (Zur Kenntniss des Milzgewebes, Müll. Arch. 1850) had confirmed and extended Müller's observations with regard to the distribution of the vessels in the Malpighian bodies. He says, p. 167, "Their framework is a vascular plexus. The larger vessels (*cylinder*) are longitudinally striated, in consequence of the regular arrangement of the nuclei upon their walls, the smaller are simple tubes." These observations were made on persons who died of cholera.

In January, 1851, Dr. Sanders read a paper, 'On the connexion of the minute Arterial Twigs with the Malpighian Sacculi in the Spleen,' before the Edinburgh Physiological Society, in which he describes a peculiar method of preparation of the pig's spleen, whereby arterial twigs may be demonstrated "passing diametrically across the area of the sacculi." "Stains of blood also, often in linear arrangement, indicating capillaries, were seen in the interior of the sacculi."

Kölliker ('Mik. Anat.' and 'Handbuch,' 1852), while denying the entrance of the arterial twigs into the Malpighian bodies, states that he had just succeeded in once observing a network of fine capillaries in those of a cat, and he supposes that they will hereafter be discovered in other animals. Finally, Mr. Wharton Jones speaks doubtfully of having observed a single capillary tube in the Malpighian bodies of the sheep. (On blood-corpuscle-holding cells.—Brit. and For. Med. Chir. Review, 1853). The existence of a special continuous membrane investing the Malpighian bodies is affirmed by Ecker, Gerlach, Kölliker, and Sanders. On the other hand, it is denied by Henle (Allg. Anat. 1001), and by Wharton Jones (l. c.).

With regard to the contents, Müller's statements, as we have seen, waver. Henle, Gerlach, Kölliker, and Sanders say that they are composed of corpuscles suspended in a fluid. The quantity of the latter is however, according to Kölliker, small.

I may now proceed to communicate the results of my own observations upon the structure of the Malpighian bodies in Man, the Sheep, Pig, Rat, and Kitten, and I will arrange what I have to say under the three heads of—1. The distribution of the vessels of the Malpighian bodies. 2. The structure of their substance (so-called contents), or the Malpighian pulp. 3. The structure of their peripheral portion, or so-called 'walls.'

1. *The Distribution of the Vessels of the Malpighian Bodies.*

In all the animals above mentioned, I find it very easy to demonstrate, in almost every case, that one or more minute arterial twigs enter and frequently subdivide in the substance of the Malpighian body, making their exit on its opposite side, to terminate, finally, by breaking up into minute branches in the pulp. Indeed, it is so easy to convince oneself of this fact, if a thin section of a fresh spleen be examined under the simple microscope, that it is difficult to understand how two opinions can exist upon the subject. The method I have adopted is simply this: to such a section I add some weak syrup, so as to retain the colouring matter in the blood-corpuscles contained in the vessels, and thus to have the advantage of a natural injection; then, I either trace out the vessels into the Malpighian bodies with needles, under a $\frac{1}{4}$-inch lens; or, placing a glass plate over the section, I apply a gentle and gradual pressure, just sufficient to render the bodies transparent. It is then easy, by sliding the plate with a needle, to cause the bodies to roll a little upon their axes, and thus convince oneself, by the relative positions which the vessels and

the bodies assume, that the former do really pass through, and not merely over, the latter. In Plate III. [Plate XXV.] (figs. 1, 2, and 7) I have represented the ordinary modes in which the arterial twigs are disposed in the Malpighian bodies of the sheep (figs. 1, 2) and of Man (fig. 7). It should be observed, however, that the Malpighian bodies have by no means always the well-marked oval outline which is here represented. On the other hand they are very frequently diffuse and irregular, sending out processes along the efferent and afferent twigs.

The application of a high power, either to the compressed Malpighian body, or to one which has been torn out with needles and its vessels isolated, fully confirms the results obtained by the previous methods. In Man, the structure of the minute arterial twigs within the bodies does not differ from that which they possess elsewhere (fig. 7). Both the transversely (smooth-muscular) and longitudinally fibrous coats are well developed, neither being in excess ; and the addition of acetic acid produces a clear line external to the former, representing the innermost portion of the *tunica adventitia*, which passes into, and is continuous with, the Malpighian pulp. The artery, therefore, is not only surrounded by, and in immediate contact with, the indifferent tissue of the pulp, but the latter, as Müller pointed out, is really the representative of a part of its *tunica adventitia*. In fact, the indifferent tissue so completely forms an integral constituent of the coat of the artery, that I could not, in any way, obtain the latter free from it.

In the Sheep, the arterial twigs have precisely the same relation to the Malpighian pulp, but the intimate structure of their walls is different, the circularly fibrous layer becoming almost obsolete, while the longitudinally fibrous coat acquires proportionally increased dimensions, and takes, at the same time, the structure of organic muscle. In the small arterial twigs of 1-800th inch in diameter, represented in fig. 3, the cavity of the vessels did not occupy more than one-third of their diameter, and, like the efferent ramuscules, unless they contained blood, they resembled mere *trabeculæ*, consisting of organic muscle.

The vessels within the Malpighian bodies are, however, not arterial ramifications only : I find that there invariably exists, in addition, a tolerably rich network of capillaries connecting the arterial ramuscules. These capillaries are vessels of 1-1000th to 1-3000th of an inch, or even less, in diameter, which can hardly be said to have parietes distinct from the surrounding indifferent tissue of the pulp (figs. 3 and 8) ; unless they are filled with blood, indeed, they are not distinguishable with certainty ; and in the figures 2 and 7, I have, there-

fore, only represented those fragments of the capillary network in which blood corpuscles were clearly distinguishable, their colouring matter being retained by the syrup. After the addition of water, it is often impossible to recognize the capillaries at all; but using syrup, I have readily enough seen them in all the animals above mentioned.

It may then perhaps be fairly concluded that, in mammals, the Malpighian bodies are traversed by minute arteries, and contain, in addition, a network of capillaries.

2. *The Structure of the "Contents" or Pulp of the Malpighian Bodies.*

Almost all writers have agreed in stating that the interior of the Malpighian bodies is filled by a liquid, consisting, as Kölliker says, of a small quantity of fluid with a large proportion of corpuscles. However, I have been quite unable to convince myself of the existence of any fluid matter at all in the interior of the perfectly-fresh Malpighian bodies of any of the animals I have examined. On the other hand, the Malpighian pulp appears to me to be as solid as any other indifferent tissue, *e.g.*, that which constitutes the lowest layer of an epidermis or epithelium, or as the most superficial portion of any dermal structure. It is, indeed, like these, soft and capable of being crushed into a semifluid substance, which becomes diffused in any surrounding liquid, like mud in water; but that it is a soft solid and not a fluid, results, I think, from what I have stated with regard to the difficulty of completely detaching it from the arterial twigs.

The essential structure of the Malpighian pulp appears to me to be that of every other indifferent tissue which I have yet examined; it consists, in fact, of a homogeneous, transparent, structureless matrix, or periplast, containing closely-set rounded or polygonal vesicular endoplasts: these vary in diameter from less than 1-5000th inch up to 1-2500th, or a little more, and contain usually one to three, but frequently many, minute granules[1] (fig. 4). On the addition of acetic acid, the periplast often becomes granular and less transparent, while the endoplasts are rendered darker and more sharply defined, undergoing a certain wrinkling. There are neither cell cavities nor cell walls distinguishable around these endoplasts, and therefore the Malpighian pulp cannot be said to be composed of 'nucleated cells;'

[1] These therefore correspond with the "nuclei" and "nucleoli" of authors. The reasons for not so denominating them are contained in an article 'On the Cell Theory' ('Brit. and For. Med. Chir. Review, October 1853'). I may observe that I know of no tissue better calculated to illustrate the view which I have there taken of Histogenesis, than the Malpighian pulp.

resembling, in this respect, all the primary, unmetamorphosed tissues with which I am acquainted.

True cells are, however, to be met with here and there in the Malpighian pulp. There is first to be observed a clear area, as of a cavity, surrounding an endoplast; the periplast forming the outer limit of this clear area then acquires a more distinct definition (fig. 5), and becomes recognizable as a cell-wall, from the remaining periplast. Such complete cells measure from 1-2500th to 1-1500th of an inch in diameter. A further change is undergone by the periplast within and around some of these cells; granules are deposited, which are sometimes minute and colourless, sometimes, on the other hand, have a deep-red colour and a considerable size, constituting the well-known 'pigment-globule-cells' of the spleen; but I may remark, that I have never been able to observe any blood corpuscles in such cells.

If the Malpighian pulp be pressed out or torn with needles, it is very readily broken up and diffused through the surrounding fluid. We then find in the latter free endoplasts—endoplasts surrounded by definite cell walls and cell cavities—and granule and pigment cells, corresponding with the elements which were observed in the uninjured tissue. That the free cells were not primarily independent structures, but have simply resulted from the breaking up of the periplast along its lines of least cohesion, is evidenced, in a very interesting manner, by such forms as are represented in fig. 6, where two cells may be observed still connected by a bridge of periplastic (or as it would here be called, in the language of the cell theory, 'intercellular') substance, while the outline of a single isolated cell is still irregular and granular, from the adhesion of particles of the periplast of which it once formed a portion. Such bodies as these are quite undistinguishable, structurally, from pus, mucus, or colourless blood corpuscles.[1]

3. *The Peripheral portion, so-called "Wall," of the Malpighian Body.*

In the human spleen, the Malpighian bodies cannot be said with any propriety to possess walls. Their structure remains, as we have described it, up to their junction with the surrounding red pulp. At

[1] The above account of the structure of the Malpighian bodies is essentially identical with that given by Mr. Wharton Jones, l. c. pp. 34, 35, but was drawn up before I had the good fortune to become acquainted with his article. He describes the wall of the nucleated cells as being "not very smooth," and the periplast as a "diffluent intercellular substance," whence I presume that I may quote him as an authority for the absence of fluid in the Malpighian bodies.

the line of junction, a somewhat more condensed tissue, which breaks up, like a great deal of the red pulp, into spindle-shaped bodies, and those fibres with onesided endoplasts, described by Kölliker, may be found ; but this tissue belongs as much to the red pulp as to the Malpighian body.

In the Sheep, on the other hand, I find, to quote Mr. Wharton Jones's words, that—

"Examined with a low magnifying power, the Malpighian corvesicles present the appearance of thick-walled, glandular vesicles, with contents. The thick walls are not defined and homogeneous, but are, on examination with a high power, found to be composed of nucleated fibres and nucleated corpuscles, similar to those of the red pulpy substance, between which, indeed, and the exterior surface of the Malpighian corpuscles there is no very distinct line of demarcation other than is produced by the condensation of the wall of the Malpighian corpuscles and the absence in them of coloration."

In addition to this, however, I find upon the exterior of the Malpighian bodies in the Sheep the mesh-work of pale fibres (fig. 2, *d'*), like very young elastic tissue, or the fibres of the zonule of zinn, to which Kölliker and Sanders have referred ; and I have occasionally met with such fibres in the interior of the bodies themselves, traversing the Malpighian pulp. They appear to me to belong to the original *tunica adventitia* of the arteries. The existence of any distinct structureless limitary membrane may, I think, be very decidedly denied ; and with regard to the "granular membrane, the internal surface of which is lined by a layer of large nucleated cells, while free nuclei or corpuscles, with a homogeneous or granular plasma, fill its interior" (Sanders, l. c., p. 35) ; all I can say is, that I cannot give any opinion as to what it may be, never having met with a Malpighian body presenting any such structures.

It may be said, then, that the Malpighian bodies of the mammalian spleen are not closed follicles, and have no analogy whatever to the acini of ordinary glands, but that they are portions of the spleen, everywhere continuous with the rest, but distinguished from it—*a*, by immediately surrounding, and as it were replacing, the *tunica adventitia* of the arteries ; *b*, by containing no wide venous sinuses, but, at most, a network of delicate capillaries ; and *c*, by being composed of absolutely indifferent tissue, *i.e.*, of a structureless periplast with imbedded endoplasts—or of a tissue in which the periplast has undergone no further metamorphosis than that into cell-wall and rudimentary fibre.

For a demonstration that each of these propositions holds good of the Malpighian bodies in the other three classes of the Vertebrata, I

must refer to Remak's very able essay, ' Ueber Pigment-kugel-hâltige Zellen,' in Müller's ' Archiv.' for 1852, and to Leydig's recent ' Untersuchungen über Fische und Reptilien,' in which ample evidence of the fact will be found ; and my limits oblige me to allude, with equal brevity, to another important doctrine which many recent writers have maintained, but which is especially enunciated and illustrated by Leydig, namely—that there is no line of demarcation to be drawn between the spleen, the lymphatic glands, Payer's patches, and the glandulæ solitariæ, the supra-renal capsules, the thymus, and the pituitary body, but that these form one great class of glands characterized essentially by being masses of indifferent tissue contained in vascular plexuses, and which may therefore well retain their old name of Vascular Glands.

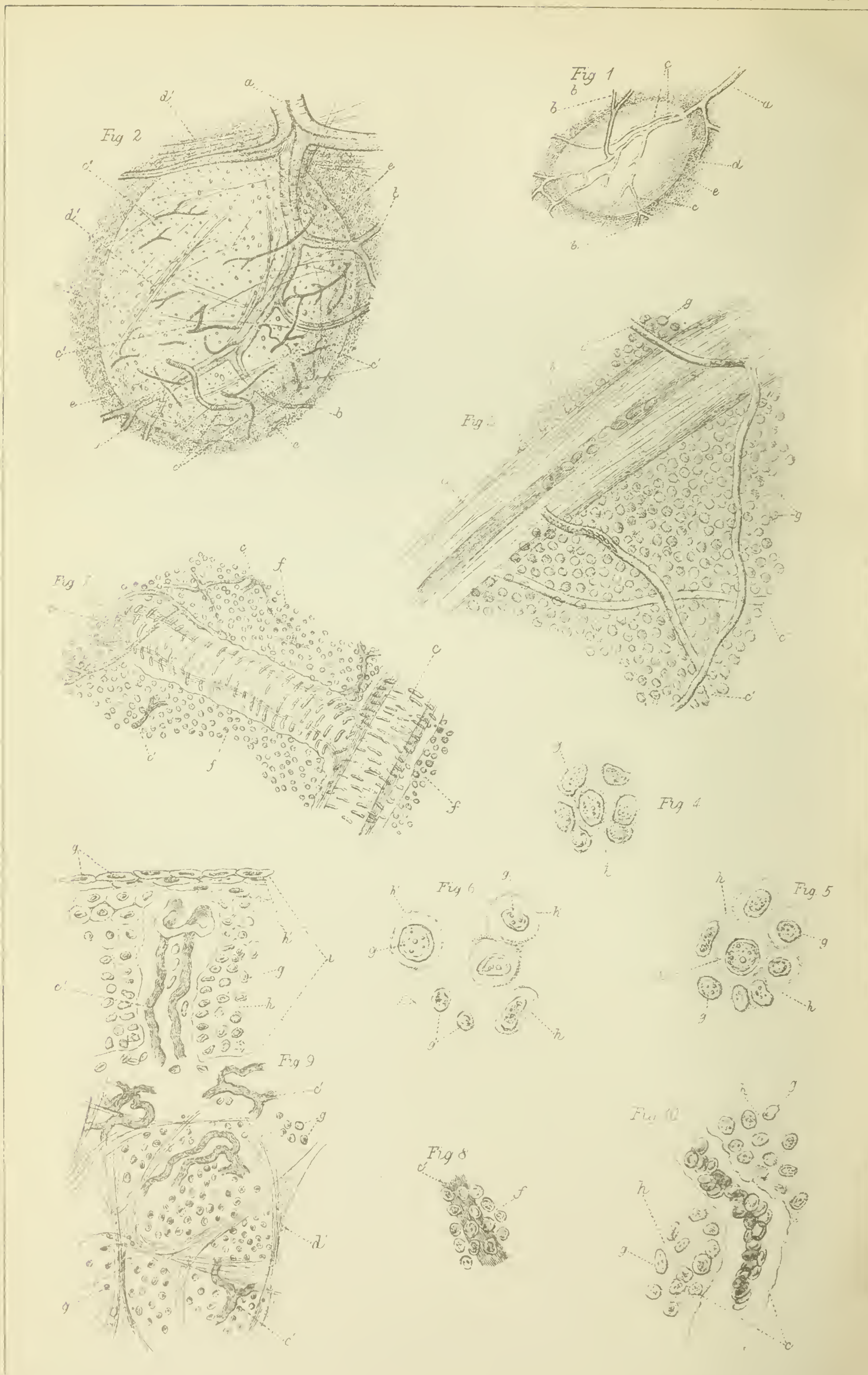
The primary form of these is represented by the solitary gland of the alimentary canal, which is nothing but a local hypertrophy of the indifferent element of the connective tissue of the part, and possesses no other capsule than that which necessarily results from its being surrounded by the latter.

A number of such bodies as these, in contiguity, constitute, if they be developed within a mucous membrane, a Payer's patch ; if within the walls of the splenic artery and its ramifications, a spleen ; if within the walls of lymphatics, a lymphatic gland ; if in the neighbourhood or within the substance (as in Fishes) of the kidney, a supra-rena body ; if in relation with a part of the brain, a pituitary body.[1] All these organs agree in possessing nothing that can be called a duct. To those, however, which are in relation with mucous membranes, Kölliker has already justly shown (' Handbuch ' and ' Mikr. Anat.') that the ' follicular ' glands of the root of the tongue and the tonsils must be added ; the former of which possess rudimentary, and the latter a tolerably perfect, system of ducts, formed by diverticula of the mucous membrane, around which the elements of the vascular gland are arranged, though they are not directly connected with them. I can fully testify to the general accuracy of Kölliker's account of the structure of the tonsils ; but I must add that I have been unable to find ' closed follicles ' either in Man or in the Sheep ; and, on the other hand, that the indifferent tissue of the so-called ' follicles ' is permeated by a network of capillaries, which have exactly the same relation to the indifferent tissue in which they are imbedded, as in the Malpighian bodies (figs. 9, 10). So far as its structure is concerned, in fact, the tonsil exactly represents a lymphatic gland, developed

[1] I purposely abstain from including in this series the thyroid and pineal glands, because I think it certain that the former, and probably, the latter have a different import.

[PLATE XXV]

To face p. 299. Micr Journ Vol. II Pl. III



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around a diverticulum of the pharyngeal mucous membrane; its 'follicles' precisely resembling the 'alveoli' of the latter, in being constituted by imperfect septa of rudimentary connective tissue, containing a solid mass of indifferent tissue, traversed by capillaries.

Can this series of '*vascular glands with false ducts*,' as they might be called, be extended by any further addition? I venture to think that it may, and that no one can thoroughly comprehend the structure of the tonsils without perceiving, at once, that there is but a step from them to the liver. A mass of indifferent tissue contained in a vascular plexus and arranged around a diverticulum of mucous membrane, is a definition which would serve as well for the liver as for the tonsil; it is, further, perfectly in accordance with that theory of the relation of the biliary ducts to the hepatic substance, which is due to Dr. Handfield Jones, and which all recent researches, both anatomical and physiological, tend to confirm, viz., that the liver is essentially a double organ, consisting of two elements, an excretory and a parenchymatous, different homologically and functionally. It seems odd that, from being a sort of histological and physiological outcasts, the Vascular Glands should turn out, if this view be correct, to be the most important and extensive class of organs in the whole body, claiming *the* gland *par excellence*, the liver—as one of their family.

DESCRIPTION OF PLATE III. [XXV.]

Figs. 1, 2, 3, 4, 5, 6 From the Malpighian body of the Sheep.
Figs. 7, 8. From that of Man.
Figs. 9, 10. From the Tonsil of Man.

The letters have throughout the same signification.

a. Afferent vessel.
b. Efferent vessel.
c. Traversing vessel.
c'. Capillaries.
d. Line of junction between Red Pulp and Malpighian body.
d'. Fibrous meshwork.
e. Red pulp.
f. Malpighian pulp.
g. Endoplasts.
h. Periplast.
h'. Cell-wall.
i. Epithelium of the tonsil cavity in the section Fig. 9; a vascular papilla is seen extending nearly to its surface.

XXVIII

ON CERTAIN ZOOLOGICAL ARGUMENTS COMMONLY ADDUCED IN FAVOUR OF THE HYPOTHESIS OF THE PROGRESSIVE DEVELOPMENT OF ANIMAL LIFE IN TIME

Friday, April 20, 1855

Roy. Inst. Proc., vol. ii., 1854–58, *pp.* 82–85

When the fact that fossilized animal forms are no *lusus naturæ*, but are truly the remains of ancient living worlds, was once fully admitted, it became a highly interesting problem to determine what relation these ancient forms of life bore to those now in existence.

The general result of inquiries made in this direction is, that the further we go back in time, the more different are the forms of life from those which now inhabit the globe, though this rule is by no means without exceptions. Admitting the difference, however, the next question is, what is its amount? Now it appears, that while the Palæozoic *species* are probably always distinct from the modern, and the *genera* are very commonly so, the *orders* are but rarely different, and the great *classes* and *sub-kingdoms* never. In all past time we find no animal about whose proper sub-kingdom, whether that of the *Protozoa*, *Radiata*, *Annulosa*, *Mollusca*, and *Vertebrata*, there can be the slightest doubt; and these great divisions are those which we have represented at the present day.

In the same way, if we consider the Classes, *e.g. Mammalia*, *Aves*, *Insecta*, *Cephalopoda*, *Actinozoa*, &c., we find absolutely no remains which lead us to establish a class type distinct from those now existing, and it is only when we descend to groups having the rank of Orders that we meet with types which no longer possess any living representatives. It is curious to remark again, that, notwithstanding

the enormous lapse of time of which we possess authentic records, the extinct ordinal types are exceedingly few, and more than half of them belong to the same class—*Reptilia.*

The extinct ordinal Reptilian types are those of the *Pachypoda*, *Pterodactyla*, *Enaliosauria*, and *Labyrinthodonta ;* nor are we at present acquainted with any other extinct order of Vertebrata. Among the *Annulosa* (including in this division the *Echinodermata*), we find two extinct ordinal types only, the *Trilobita* and the *Cystideæ.*

Among the *Mollusca* there is absolutely *no* extinct ordinal type ; nor among the *Radiata* (*Actinozoa* and *Hydrozoa*) ; nor is there any among the *Protozoa.*

The naturalist who takes a wide view of fossil forms, in connection with existing life, can hardly recognise in these results anything but strong evidence in favour of the belief that a general uniformity has prevailed among the operations of Nature, through all time of which we have any record.

Nevertheless, whatever the amount of the difference, and however one may be inclined to estimate its value, there is no doubt that the living beings of the past differed from those of the present period ; and again, that those of each great epoch have differed from those which preceded, and from those which followed them. That there has been a succession of living forms in time, in fact, is admitted by all ; but to the inquiry—What is the law of that succession ? different answers are given ; one school affirming that the law is known, the other that it is for the present undiscovered.

According to the affirmative doctrine, commonly called the theory of Progressive Development, the history of life, as a whole, in the past, is analogous to the history of each individual life in the present ; and as the law of progress of every living creature now is from a less perfect to a more perfect, from a less complex to a more complex state—so the law of progress of living nature in the past was of the same nature ; and the earlier forms of life were less complex, more embryonic, than the later. In the general mind this theory finds ready acceptance, from the falling in with its popular notion, that one of the lower animals, *e.g.* a fish, is a higher one, *e.g.* a mammal, arrested in development ; that it is, as it were, less trouble to make a fish than a mammal. But the speaker pointed out the extreme fallacy of this notion ; the real law of development being, that the progress of a higher animal in development is not through the forms of the lower, but through forms which are common to both lower and higher : a fish, for instance, deviating as widely from the common Vertebrate plan as a mammal.

The Progression theory, however, after all, resolves itself very nearly into a question of the structure of fish-tails. If, in fact, we enumerate the oldest known undoubted animal remains, we find them to be *Graptolites*, *Lingulæ*, *Phyllopoda*, *Trilobites*, and *Cartilaginous fishes.*

The *Graptolites*, whether we regard them as *Hydrozoa*, *Anthozoa*, or *Polyzoa* (and the recent discoveries of Mr. Logan would strongly favour the opinion that they belong to the last division), are certainly in no respect embryonic forms. Nor have any traces of *Spongiadæ* or *Foraminifera* (creatures unquestionably far below them in organization), been yet found in the same or contemporaneous beds. *Lingulæ*, again, are very aberrant *Brachiopoda*, in nowise comparable to the embryonic forms of any mollusk; *Phyllopods* are the highest *Entomostraca;* and the *Hymenocaris vermicauda* discovered by Mr. Salter in the Lingula beds, is closely allied to *Nebalia*, the highest Phyllopod, and that which approaches most nearly to the *Podopthalmia.* And just as *Hymenocaris* stands between the other *Entomostraca* and the *Podopthalmia*, so the *Trilobita* stand between the *Entomostraca* and the *Edriopthalmia.* Nor can anything be less founded than the comparison of the *Trilobita* with embryonic forms of *Crustacea;* the early development of the ventral surface and its appendages being characteristic of the latter; while it is precisely these parts which have not yet been discovered in the *Trilobita*, the dorsal surface, last formed in order of development, being extremely well developed.

The *Invertebrata* of the earliest period, then, afford no ground for the Progressionist doctrine. Do the Vertebrata?

These are cartilaginous fish. Now, Mr. Huxley pointed out that it is admitted on all sides that the brain, organs of sense, and reproductive apparatus, are much more highly developed in these fishes than any others; and he quoted the authority of Prof. Owen,[1] to the effect that no great weight is to be placed upon the cartilaginous nature of the skeleton as an embryonic character. There remained, therefore, only the heterocercality of the tail, upon which so much stress has been laid by Prof. Agassiz. The argument made use of by this philosopher may be thus shortly stated:—Homocercal fishes have in their embryonic state heterocercal tails; therefore, heterocercality is, so far, a mark of an embryonic state as compared with homocercality; and the earlier, heterocercal fish are embryonic as compared with the later, homocercal.

[1] Lectures on the Comparative Anatomy of the Vertebrata, pp. 146–7.

The whole of this argument was based upon M. Vogt's examination of the development of the *Coregonus*, one of the *Salmonidæ;* the tail of *Coregonus* being found to pass through a so-called heterocercal state in its passage to its perfect form.[1] For the argument to have any validity, however, two conditions are necessary. 1. That the tails of the *Salmonidæ* should be homocercal, in the same sense as those of other homocercal fish. 2. That they should be really heterocercal, and not homocercal, in their earliest condition. On examination, however, it turns out that neither of these conditions holds good. In the first place, the tails of the *Salmonidæ*, and very probably of all the *Physostomi* are not homocercal at all, but to all intents and purposes intensely heterocercal: the chorda dorsalis in the Salmon, for instance, stretching far into the upper lobe of the tail. The wide difference of this structure from true homocercality is at once obvious, if the tails of the *Salmonidæ* be compared with those of *Scomber scombrus*, *Gadus æglefinus*, &c. In the latter, the tail is truly homocercal, the rays of the caudal fin being arranged symmetrically above and below the axis of the spinal column.

All M. Vogt's evidence, therefore, goes to show merely that a *heterocercal* fish is heterocercal at a given period of embryonic life; and in no way affects the truly homocercal fishes.

In the second place, it appears to have been forgotten that, as M. Vogt's own excellent observations abundantly demonstrate, this heterocercal state of the tail is a comparatively late one in *Coregonus*, and that, at first, the tail is perfectly symmetrical, *i.e.* homocercal.

In fact, all the evidence on fish development which we possess is to the effect that Homocercality is the younger, Heterocercality the more advanced condition: a result which is diametrically opposed to that which has so long passed current, but which is in perfect accordance with the ordinary laws of development; the asymmetrical being, as a rule, subsequent in the order of development to the symmetrical.

The speaker then concluded by observing that a careful consideration of the facts of Palæontology seemed to lead to these results:

1. That there is no real parallel between the successive forms assumed in the development of the life of the individual at

[1] Von Bär had already pointed out this circumstance in *Cyprinus*, and the relation of the fœtal tail to the permanent condition in cartilaginous fishes.—See his "Entwickelungsgeschichte der Fische," p. 36.

present, and those which have appeared at different epochs in the past; and

2. That the particular argument supposed to be deduced from the heterocercality of the ancient fishes is based on an error, the evidence from this source, if worth anything, tending in the opposite direction.

At the same time, while freely criticising what he considered to be a fallacious doctrine, Mr. Huxley expressly disclaimed the slightest intention of desiring to depreciate the brilliant services which its original propounder had rendered to science.

XXIX

ON NATURAL HISTORY, AS KNOWLEDGE, DISCIPLINE, AND POWER

Roy. Inst. Proc., vol. ii., 1854–58, *pp.* 187–195, *Friday, February* 15, 1856

THE value of any pursuit depends upon the extent to which it fulfils one or all of three conditions. Either it enlarges our experience; or it increases our strength; or it diminishes the obstacles in the way of our acquiring experience and strength. Whatever neither teaches, nor strengthens, nor helps us, is either useless or mischievous. The scientific calling, like all others, must be submitted to these tests, if we desire fairly to estimate its dignity and worth; and as the object of the present discourse is to set forth such an estimate of the science of Natural History, it will be necessary to consider—Firstly, its scope and range as mere *knowledge;* Secondly, the amount to which the process of acquiring Natural History knowledge strengthens and develops the powers of the gainer,—its position, that is, as *discipline;* Thirdly, the extent to which it enables him, so to speak, to turn one part of the universe against another, in order to attain his own ends; and this is what is commonly called the *power* of science.

There can be little doubt as to which is the highest and noblest of these standards of value. Science, as power, indeed, showers daily blessings upon our practical life; and science, as knowledge, opens up continually new sources of intellectual delight. But neither knowing nor enjoying are the highest ends of life. Strength—capacity of action and of endurance—is the highest thing to be desired; and this is to be obtained only by careful discipline of all the faculties, by that training which the pursuit of science is, above all things, most competent to give.

First, let us regard Natural History as mere Knowledge.

The common conception of the aims of a naturalist of the present

day does him great injustice, although it might perhaps fairly apply to one of a century and a half ago; when natural history, which began in the instinctive observation of the habits, and the study of the forms, of living beings, had hardly passed beyond the stage of more or less accurate anecdotes, and larger or smaller collections of curiosities.

The difference between the ancient naturalist and his modern successor is similar to that between the Chaldæan watcher of the stars and the modern astronomer; but the scientific progress of the race is epitomized in that of the individual, and may be best exemplified, perhaps, by tracing out the lines of inquiry into which any person of intelligence, who should faithfully attempt to solve the various problems presented by any living being, however simple and however humble, would necessarily be led. By the investigation of habits, the inquirer is insensibly led into Physiology, Psychology, Geographical and Geological distribution; by the investigation of the relations of forms, he is no less necessarily impelled into systematic Zoology and Botany, into Anatomy, Development, and Morphology, or Philosophical Anatomy. Now each of these great sciences is, if followed out into all its details, the sufficient occupation of a lifetime; but in their aggregate only, are they the equivalent of the science of natural history: and the title of naturalist, in the modern sense, is deserved only by one who has mastered the principles of all.

So much for the range of natural history. If we consider, not merely the number, but the nature of the problems which it presents, we shall find that they open up fields of thought unsurpassable in interest and grandeur. For instance, morphology demonstrates that the innumerable varieties of the forms of living beings are modelled upon a very small number of common plans or types. ("*Haupt-Typen*," of Von Bär, whose idea and term are merely paraphrased by "archetype," common plan, &c.) In the animal world we find only five of these common plans, that of the *Protozoa*, of the *Cœlenterata*, of the *Mollusca*, of the *Annulosa*, and of the *Vertebrata*. Not only are all animals existing in the present creation organized according to one of these five plans; but palæontology tends to show that in the myriads of past ages of which the earth's crust contains the records, no other plan of animal form made its appearance on our planet. A marvellous fact, and one which seems to present no small obstacle in the way of the notion of the possibly fortuitous development of animal life.

Not merely does the study of morphology lead us into the depths of past time, but it obliges us to gaze into that greater abyss which

lies between the human mind and that mind of which the universe is but a thought and an expression. For man, looking from the heights of science into the surrounding universe, is as a traveller who has ascended the Brocken and sees, in the clouds, a vast image, dim and awful, and yet in its essential lineaments resembling himself. In the words of the only poet of our day who has fused true science into song, the philosopher, looking into Nature,

> " Sees his shadow glory-crowned,
> He sees himself in all he sees."
>
> *Tennyson's* "*In Memoriam.*"

The mathematician discovers in the universe a "Divine Geometry;" the physicist and the chemist everywhere find that the operations of nature may be expressed in terms of the human intellect ; and, in like manner, among living beings, the naturalist discovers that their "vital" processes are not performed by the gift of powers and faculties entirely peculiar and irrespective of those which are met with in the physical world ; but that they are built up and their parts adapted together, in a manner which forcibly reminds us of the mode in which a human artificer builds up a complex piece of mechanism, by skilfully combining the simple powers and forces of the matter around him. The numberless facts which illustrate this truth are familiar to all, through the works of Paley and the natural theologians, whose arguments may be summed up thus—that the structure of living beings is, in the main, such as would result from the benevolent operation, under the conditions of the physical world, of an intelligence similar in kind, however superior in degree, to our own. Granting the validity of the premises, that from the similarity of effects we may argue to a similarity of cause, does natural history allow our conclusions to rest here? Is this utilitarian adaptation to a benevolent purpose the chief or even the leading feature of that great shadow, or, we should more rightly say, of that vast archetype of the human mind, which everywhere looms upon us through nature? The reply of natural history is clearly in the negative. She tells us that utilitarian adaptation to purpose is not the greatest principle worked out in nature, and that its value, even as an instrument of research, has been enormously overrated.

How is it then, that not only in popular works, but in the writings of men of deservedly high authority, we find the opposite dogma—that the principle of adaptation of means to ends is the great instrument of research in natural history—enunciated as an axiom? If we trace out the doctrine to its fountain head, we shall find that it was primarily put forth by Cuvier—the prince of modern naturalists. Is

it to be supposed then that Cuvier did not himself understand the methods by which he arrived at his great results? that his master-mind misconceived its own processes? This conclusion appears to be not a little presumptuous; but if the following arguments be justly reasoned out, it is correct.

In the famous "Discours sur les Révolutions de la Surface du Globe," after speaking of the difficulties in the way of the restoration of vertebrate fossils, Cuvier goes on to say—

"Happily, comparative anatomy possesses a principle whose just development is sufficient to dissipate all difficulties; it is that of the correlation of forms in organized beings, by means of which every kind of organized being might, strictly speaking, be recognised by a fragment of any of its parts.

"Every organized being constitutes a whole, a single and complete system, whose parts mutually correspond, and concur, by their reciprocal reaction, to the same definite end. None of these parts can be changed without affecting the others; and consequently, each taken separately indicates and gives all the rest."

After this Cuvier gives his well-known examples of the correlation of the parts of a carnivore, too long for extract; and of which therefore his summation merely will be given:—

"In a word, the form of the tooth involves that of the condyle; that of the shoulder blade; that of the claws: just as the equation of a curve involves all its properties. And just as by taking each property separately and making it the base of a separate equation, we should obtain both the ordinary equation, and all other properties whatsoever which it possesses; so, in the same way, the claw, the scapula, the condyle, the femur, and all the other bones taken separately will give the tooth, or one another; and by commencing with any one, he who had a rational conception of the laws of the organic economy, could reconstruct the whole animal."

Thus far Cuvier: and thus far and no further, it seems that the compilers, and copyers, and popularizers, and *id genus omne*, proceed in the study of him. And so it is handed down from book to book, that all Cuvier's restorations of extinct animals were affected by means of the principle of the physiological correlation of organs.

Now let us examine this principle; taking in the first place, one of Cuvier's own arguments and analyzing it; and in the second place, bringing other considerations to bear.

Cuvier says—"It is readily intelligible that ungulate animals must all be herbivorous, since they possess no means of seizing a prey (1). We see very easily also, that the only use of their fore feet

being to support their bodies, they have no need of so strongly formed a shoulder; whence follows the absence of clavicles (2) and acromion, and the narrowness of the scapula. No longer having any need to turn their fore-arm, the radius will be united with the ulna, or least articulated by a ginglymus and not arthrodially with the humerus (3). Their herbivorous diet will require teeth, with flat crowns, to bruise up the grain and herbage; these crowns must needs be unequal, and to this end enamel must alternate with bony matter (4); such a kind of crown requiring horizontal movements for trituration, the condyle of the jaw must not form so close a hinge as in the carnivora; it must be flattened; and this entails a correspondingly flattened temporal facet. The temporal fossa which will have to receive only a small temporal muscle will be shallow and narrow (5)."

The various propositions are here marked with numbers, to avoid repetition; and it is easy to show that not one is really based on a necessary physiological law:—

> (1.) Why should not ungulate animals be carrion feeders? or even, if living animals were their prey, surely a horse could run down and destroy other animals with at least as much ease as a wolf.
>
> (2, 3.) But what purpose, save support, is subserved by the forelegs of the dog and wolf? how large are their clavicles? how much power have they of rotating the fore-arm?
>
> (4, 5.) The sloth is purely herbivorous, but its teeth present no trace of any such alternation of substance.

Again, what difference exists in structure of tooth, in the shape of the condyle of the jaw, and in that of the temporal fossa, between the herbivorous and carnivorous bears? If bears were only known to exist in the fossil state, would any anatomist venture to conclude from the skull and teeth alone, that the white bear is naturally carnivorous, while the brown bear is naturally frugivorous? Assuredly not; and thus, in the case of Cuvier's own selection, we see that his arguments are absolutely devoid of conclusive force. Let us select another then: on the table is a piece of carboniferous shale, bearing the impression of an animal long since extinct. It is a mere impression of the external form, but this is amply sufficient to enable us to be morally certain that if we had a living specimen, we should find its jaws, if it had any, moving sideways—that its hard skeleton formed a sheath outside its muscles—that its nervous system was turned downwards when it walked—that the heart was placed on the opposite side of the body—that if it possessed special respiratory organs, they were gills, &c., &c.

In fact, we have in the outward form abundant material for the restoration of the internal organs. But how do we conclude, from the peculiar many-ringed body, with jointed limbs, of this ancient marine animal, that it had all these other peculiarities; in short, that it was a crustacean? For any physiological necessity to the contrary, the creature might have had its mouth, nervous system, and internal organs arranged like those of a fish. We know that it was a crustacean and not a fish, simply because the observation of a vast number of instances assures us that an external structure such as this creature possesses, is invariably accompanied by the internal peculiarities enumerated. Our method then is not the method of adaptation, of necessary physiological correlations; for of such necessities, in the case in question, we know nothing: but it is the method of agreement; that method by which, having observed facts invariably occur together, we conclude they invariably have done so, and invariably will do so; a method used as much in the common affairs of life as in philosophy.

Multitudes of like instances could be adduced from the animal world; and if we turn to the botanist, and inquire how he restores fossil plants from their fragments, he will say at once that he knows nothing of physiological necessities and correlations. Give him a fragment of wood, and he will unhesitatingly tell you what kind of a plant it belonged to, but it will be fruitless to ask him what physiological necessity combines, *e.g.* peculiarly dotted vessels, with fruit in the shape of a cone and naked ovules, for he knows of none. Nevertheless, his restorations stand on the same logical basis as those of the zoologist.

Therefore, whatever Cuvier himself may say, or others may repeat, it seems quite clear that the principle of his restorations was *not* that of the physiological correlation or coadaptation of organs. And if it were necessary to appeal to any authority, save facts and reason, our first witness should be Cuvier himself, who, in a very remarkable passage, two or three pages further on (Discours, pp. 184–185,[1]) implicitly surrenders his own principle.

Thus then natural history plainly teaches us that the utilitarian principle, valuable enough in physiology, helps us no further, and is utterly insufficient as an instrument of morphological research.

But does she then tell us that in this, her grander sphere, the human mind discovers no reflex, and that among those forms of being which most approach himself alone, man can discover no indication

[1] Ossemens Fossiles, 4me édition, T. I.

of that vast harmony with his own nature which seemed so obvious elsewhere? Surely not. On the contrary, it may be regarded as one of the noblest characteristics of natural history knowledge, that its highest flights point, not to a discrepancy between the infinite and the finite mind, but to a higher and closer union than can be imagined by those whose studies are confined to the physical world. For where the principle of adaptation, of mere mechanical utilitarian contrivance fails us, it is replaced by another which appeals to the æsthetic sense as much as the mere intellect.

Regard a case of birds, or of butterflies, or examine the shell of an echinus, or a group of foraminifera, sifted out of the first handful of sea sand. Is it to be supposed for a moment that the beauty of outline and colour of the first, the geometrical regularity of the second, or the extreme variety and elegance of the third, are any *good* to the animals? that they perform any of the actions of their lives more easily and better for being bright and graceful, rather than if they were dull and plain? So, to go deeper, is it conceivable that the harmonious variation of a common plan which we find everywhere in nature serves any utilitarian purpose? that the innumerable varieties of antelopes, of frogs, of clupeoid fishes, of beetles, and bivalve mollusks, of polyzoa, of actinozoa, and hydrozoa, are adaptations to as many different kinds of life, and consequently varying physiological necessities? Such a supposition with regard to the three last, at any rate, would be absurd; the polyzoa, for instance, presenting a remarkable uniformity in mode of life and internal organization, while nothing can be more striking than the wonderful variety of their external shape and of the sculpture of their cells. If we turn to the vegetable world, we find it one vast illustration of the same truth. Who has ever dreamed of finding an utilitarian purpose in the forms and colours of flowers, in the sculpture of pollen-grains, in the varied figures of the frond of ferns? What "purpose" is served by the strange numerical relations of the parts of plants, the threes and fives of monocotyledons and dicotyledons?

Thus in travelling from one end to the other of the scale of life, we are taught one lesson, that living nature is not a mechanism but a poem; not a mere rough engine-house for the due keeping of pleasure and pain machines, but a palace whose foundations, indeed, are laid on the strictest and safest mechanical principles, but whose superstructure is a manifestation of the highest and noblest art.

Such is the plain teaching of Nature. But if we have a right to conclude from the marks of benevolent design to an infinite

Intellect and Benevolence, in some sort similar to our own, then from the existence of a beauty (nay, even of a humour), and of a predominant harmonious variety in unity in nature, which, if the work of man, would be regarded as the highest art, we are similarly bound to conclude that the æsthetic faculties of the human soul have also been foreshadowed in the Infinite Mind.

Such is a brief indication of the regions of thought into which natural history leads us, and we may surely conclude that as *Knowledge* it stands second in scope and breadth to no science.

As *Discipline*, impartial consideration will show that it takes no lower rank; whether we regard it as a gymnastic for the intellectual, the moral, or the æsthetic faculty.

For the successful carrying on of the business of life, no less than for the pursuit of science, it is essential that the mind should easily and accurately perform the four great intellectual processes of observation, experiment, induction, and deduction. No training can be so well adapted to develop the first of these faculties as that of the naturalist, the very foundation of whose studies lies in exact observation of characters and nice discrimination of resemblances and differences. In fact, the skilled naturalist is the only man who combines the moral and intellectual advantages of civilization with that acuteness and minute accuracy of perception which distinguish the savage hunter; and if man's senses are to keep pace with his intellect as the world grows older, natural history observation must be made a branch of ordinary education.

Again, what science can present more perfect examples of the application of the methods of experiment than physiology? All that we know of the physiology of the nervous system rests on experiment; and if we turn to other functions, the investigations of Bernard might be cited as striking specimens of experimental research.

To say that natural history as a science is equivalent to the assertion that it exercises the inductive and deductive faculties; but it is often forgotten that the so-called "natural classification" of living beings is, in reality, not mere classification, but the result of a great series of inductive investigations. In a "natural classification" the definitions of the classes are, in fact, the laws of living form, obtained, like all other laws, by a process of induction from observed facts.

For examples of the exercise of deduction, of the arguing from the laws of living form obtained by induction, to their legitimate consequences, the whole science of palæontology may be cited.

As has been already shown, the whole process of palæontological restoration depends—First, on the validity of a law of the invariable coincidence of certain organic peculiarities established by induction; Secondly, on the accuracy of the logical process of deduction from this law. Professor Owen's determination of the nature of the famous Stonesfield mammal is a striking illustration of this. A small jaw of a peculiar shape was found, containing a great number of teeth, some of which were imbedded by double fangs in the jaw.

Now these laws have been inductively established—

(*a*) That only mammals have teeth imbedded in a double socket.

(*b*) That only marsupials have teeth in so great a number, imbedded in so peculiarly formed a jaw.

By deduction from these laws to the case in question, the legitimate conclusion was arrived at, that the jaw belonged to a marsupial mammal.

The naturalist then, who faithfully follows his calling leaves no side of his intellect untrained; but, after all, intellect, however gigantic, confers but half the qualifications required by one who desires to follow science with success, and he who gains only knowledge from her, gains but little. The moral faculties of courage, patience, and self-denial, are of as much value in science as in life; the origin of an erroneous doctrine lies as often in the heart as in the head; and the basis of the character of a great philosopher will commonly be found, on close analysis, to be earnest truthfulness—and no imaginary gift of genius. It is character and not talent which is the essential element of success in science. But as the muscle of the smith grows stronger by reason of its constant use in hammering, so it seems impossible to doubt that the training of the moral faculty, necessarily undergone by the philosopher, must react upon the man. There are, indeed, lamentable examples of men who seem to have one moral faculty for science, and another for their daily affairs: but such instances are hardly found in the highest ranks of philosophy; and when they occur, the daily poison may be traced spreading higher and higher, and sooner or later falling like a Nemesis upon the scientific faculty.

Let those who doubt the efficacy of science as moral discipline make the experiment of trying to come to a comprehension of the meanest worm or weed, of its structure, its habits, its relation to the great scheme of nature. It will be a most exceptional case, if the mere endeavour to give a correct outline of its form, or to describe its appearance with accuracy, do not call into exercise far more patience,

perseverance, and self-denial than they have easily at command; and if they do not rise up from the attempt, in utter astonishment at the habitual laxity and inaccuracy of their mental processes, and in some dismay at the pertinacious manner in which their subjective conceptions and hasty preconceived notions interfere with their forming a truthful conception of objective fact. There is not one person in fifty whose habits of mind are sufficiently accurate to enable him to give a truthful description of the exterior of a rose.

Finally, the *power* of natural history was illustrated by examples of recent applications of that science in opening up sources of industrial wealth.

XXX

ON THE PRESENT STATE OF KNOWLEDGE AS TO THE STRUCTURE AND FUNCTIONS OF NERVE

Roy. Inst. Proc., vol. ii., 1854-58, *pp.* 432–437, *Friday, May* 15, 1857

THE speaker commenced by directing the attention of the audience to an index, connected with a little apparatus upon the table, and vibrating backwards and forwards with great regularity. The cause of this motion was the heart of a frog (deprived of sensation though not of life) which had been carefully exposed by opening the pericardium, and into whose apex the point of a needle connected with the index had been thrust. Under these circumstances the heart would go on beating, with perfect regularity and full force, for hours; and as every pulsation caused the index to travel through a certain arc, the effect of any influences brought to bear upon the heart could be made perfectly obvious to every one present.

The frog's heart is a great hollow mass of muscle, consisting of three chambers, a ventricle and two auricles, the latter being separated from one another by a partition or septum. By the successive contraction of these chambers the blood is propelled in a certain direction; the auricles contracting force the blood into the ventricle; the ventricle then contracting drives the blood into the aortic bulb; and it is essential to the full efficiency of the heart as a circulatory organ; that all the muscular fibres of the auricles should contract together; and that all the muscular fibres of the ventricle should contract together; but that the latter should follow the former action after a certain interval.

The contractions of the muscles of the heart thus occur in a definite order, and exhibit a combination towards a certain end. They are rhythmical and purposive; and it becomes a question of

extreme interest to ascertain, where lies the regulative power which governs their rhythm.

If we examine into the various structures of which the heart is composed, we find that the bulk of the organ is made up of striped muscular fibres, bound together as it were by connective tissue, and lined internally and externally by epithelium. Now it is certain that the regulative power is not to be found in any of these tissues. The two latter may, for the present purpose, be regarded as unimportant, as they certainly take no share either in producing or guiding the movements of the heart. The muscular tissue, on the other hand, though the seat of the contractility of the organ, requires some influence from without, some stimulus, in order to contract at all, and having once contracted, it remains still until another stimulus excites it. There is, therefore, nothing in its muscular substance which can account for the constantly recurring rhythmical pulsations of the heart.

Experiments have been made, however, which clearly show that the regulative power is seated, not only in the heart itself, but in definite regions of the organ. Remove the heart from the body, and it still goes on beating; the source of the rhythm is therefore to be sought in itself. If the heart be halved by a longitudinal section, each half goes on beating; but if it be divided transversely, between the line of junction of the auricles with the ventricle and the apex of the latter, the detached apex pulsates no longer, while the other segment goes on beating as before. If the section be carried transversely through the auricles, both segments go on beating; and if the heart be cut into three portions by two transverse sections, one above the junction of the auricles and ventricle, and one below it, then the basal and middle segments will go on pulsating, while the apical segment is still. Clearly then, the source of the rhythmical action, the regulative power, is to be sought somewhere about the base of the auricles, and somewhere about the junction of the auricles and ventricles.

Now there is in the frog's heart, besides the three tissues which have been mentioned, a fourth, the nervous tissue. A ganglion is placed at the base of the heart, where the great veins enter the auricles—from this two cords can be traced traversing the auricular septum, and entering two other ganglia placed close to the junction of the auricles with the ventricles. From these ganglia nerves are distributed to the muscular substance. Now we know, from evidence afforded by other striped muscles and nerves, that the contraction of the former is the result of the excitement of the latter; in like

manner, we know that the ganglia are centres whence that excitement originates. We are therefore justified, analogically, in seeking for the sources of the contractions of the cardiac muscles, in the cardiac ganglia; and the experiments which have been detailed—by showing that the rhythmical contractions continue in any part of the heart which remains connected with these ganglia, while it ceases in any part cut off from them—prove that they really are the seats of the regulative power.

The speaker then exhibited another very remarkable experiment (first devised by Weber) which leads indirectly to the same conclusion. An electro-magnetic apparatus was so connected with the frog upon the table, that a series of shocks could be transmitted through the pneumogastric nerves. When this was done, it was seen that the index almost instantly stopped, and remained still, so long as the shocks were continued; on breaking contact, the heart remained at rest for a little time, then gave a feeble pulsation or two, and then resumed its full action. This experiment could be repeated at will, with invariably the same results; and it was most important to observe, that during the stoppage of the heart the index remained at the lowest point of its arc, a circumstance which, taken together with the distended state of the organ, showed that its stoppage was the result, not of tetanic contraction but of complete relaxation.

Filaments of the pneumogastric nerve can be traced down to the heart, and whenever these fibres are irritated the rhythmical action ceases. The pneumogastric nerves must act either directly upon the muscles of the heart, or indirectly through the ganglia, into which they can be traced. If the former alternative be adopted, then we must conceive the action of the pneumogastric nerve upon muscle to be the reverse of that of all other nerves—for irritation of every other muscular nerve causes activity and not paralysis of the muscle. Not only is this in the highest degree improbable, but it can be demonstrated to be untrue; for on irritating, mechanically, the surface of the heart brought to a standstill by irritation of the pneumogastrics, it at once contracts. The paralysing influence therefore is not exerted on the muscles, and as a consequence, we can only suppose that this "negative innervation," as it might be conveniently termed, is the result of the action of the pneumogastric on the ganglia.

It results from all these experiments, firstly, that nerve substance possesses the power of exciting and co-ordinating muscular actions; and secondly, that one portion of nervous matter is capable of controlling the action of another portion. In the case of the heart it is perfectly clear that consciousness and volition are entirely

excluded from any influence upon the action of the nervous matter, which must be regarded as a substance exhibiting certain phenomena, whose laws are as much a branch of physical inquiry as those presented by a magnet.

Now (still carefully excluding the phenomena of consciousness), we shall find on careful examination, that all the properties of Nerve are of the same order as those exhibited by the nervous substance of the heart. Every action is a muscular action, whose proximate cause is the activity of a nerve, and as the muscles of the heart are related to its ganglia, so are the muscles of the whole body related to that great ganglionic mass which constitutes the spinal marrow, and its continuation the medulla oblongata. This cranio-spinal nervous centre originates and co-ordinates the contractions of all the muscles of the body independently of consciousness, and there is every reason to believe that the organ of consciousness stands related to it as the pneumogastric is related to the cardiac ganglia; that volition whether it originates, or whether it controls action, exerts its influence not directly on the muscles but indirectly upon the cranio-spinal ganglia. A volition is a conscious conception, a desire; an act is the result of the automatic unconscious origination and co-ordination, by the cranio-spinal ganglia, of the nervous influences required to produce certain muscular contractions.

Whatever may be the ultimate cause of our actions then, the proximate cause lies in nerve substance. The nervous system is a great piece of mechanism placed between the external world and our consciousness; through it objects affect us; through it we affect them; and it therefore becomes a matter of the highest interest to ascertain how far the properties and laws of action of nerve substance have been ascertained by the physiological philosopher.

Nerve substance has long been known to consist of two elements, fibres and ganglionic corpuscles. Nerve fibres are either sensory or motor, and the activity of any one fibre does not influence another. But when nerve fibres come into relation with ganglionic corpuscles, the excitement of a sensory nerve gives rise to that of a motor nerve, the ganglionic corpuscles acting in some way as the medium of communication. The "grey matter" which occupies the middle of the spinal marrow has long been known to be the locality in which the posterior roots, or sensory fibres, of the nerves of the body, and the anterior roots, or motor fibres, come into relation with ganglionic corpuscles; and as the channel by which, in what are called reflex actions, the activity of the sensory nerves is converted into excitement of corresponding motor nerves. The precise *modus operandi* of the

grey matter has been much disputed, but the recent researches of Wagner, Bidder, Kupfer, and Owsjannikow, throw a great light upon, and vastly simplify the whole problem. It would appear that all nerve fibres are processes of ganglionic corpuscles; that, in the spinal cord, the great mass of the grey matter is nothing but connective tissue, the true ganglionic corpuscles being comparatively few, and situated in the anterior horns of the grey substance; finally, it would seem that no ganglionic corpuscle has more than five processes; one, which becomes a sensory fibre and enters the posterior roots of the nerves; one, a motor fibre which enters the anterior roots; one, which passes upward to the brain; one, which crosses over to a ganglionic corpuscle in the other half of the cord; and perhaps one establishing a connection with a ganglionic corpuscle on the same side.

It is impossible to overrate the value of these discoveries; for if they are truths, the problem of nervous action is limited to these inquiries: (*a*) What are the properties of ganglionic corpuscles? (*b*) What are the properties of their two, or three, commissural processes? For we are already pretty well acquainted with the properties of the sensory and motor processes.

A short account was next given of the physical and physiological phenomena exhibited by active and inactive nerve; and the phenomena exhibited by active nerve were shown to be so peculiar as to justify the application of the title of "nerve force" to this form of material energy.

It was next pointed out that this force must be regarded as of the same order with other physical forces. The beautiful methods by which Helmholtz has determined the velocity (not more than about 80 feet in a second in the frog), with which the nervous force is propagated were explained. It was shown that nerve force is not electricity, but two important facts were cited to prove that the nerve force is a correlate of electricity, in the same sense as heat and magnetism are said to be correlates of that force. These facts were, firstly, the "negative deflection" of Du Bois Raymond, which demonstrates that the activity of nerve affects the electrical relations of its particles; and secondly, the remarkable experiments of Eckhard (some of which the speaker had exhibited in his Fullerian course) which prove that the transmission of a constant current along a portion of a motor nerve so alters the molecular state of that nerve as to render it incapable of exciting contraction when irritated.

These facts, even without those equally important though less thoroughly understood experiments of Ludwig and Bernard, which

appear to indicate a direct relation between nerve force and chemical change, seem sufficient to prove that nerve force must henceforward take its place among the other physical forces.

This then is the present state of our knowledge of the structure and functions of nerve. We have reason to believe in the existence of a nervous force, which is as much the property of nerve as magnetism is of certain ores of iron; the velocity of that force is measured; its laws are, to a certain extent, elucidated; the structure of the apparatus through which it works promises soon to be unravelled; the directions for future inquiry are limited and marked out; the solution of all problems connected with it is only a question of time.

Science may be congratulated on these results. Time was when the attempt to reduce vital phenomena to law and order was regarded as little less than blasphemous: but the mechanician has proved that the living body obeys the mechanical laws of ordinary matter; the chemist has demonstrated that the component atoms of living beings are governed by affinities, of one nature with those which obtain in the rest of the universe; and now the physiologist, aided by the physicist, has attacked the problem of nervous action—the most especially vital of all vital phenomena—with what result has been seen. And thus from the region of disorderly mystery, which is the domain of ignorance, another vast province has been added to science, the realm of orderly mystery.

XXXI

ON THE PHENOMENA OF GEMMATION

Abstract of a Friday Evening Discourse at the Royal Institution, May 21, 1858; *Roy. Inst. Proc. vol. ii.* 1854–58, *pp.* 534–538; *Silliman, Journ. xxviii.*, 1859, *pp.* 206–209

THE speaker commenced by stating that a learned French naturalist, M. Duvau, proposed many years ago, to term the middle of the eighteenth century, "l'Epoque des Pucerons;" and that the importance of the phenomena which were first brought to light by the study of these remarkable insects renders the phrase "Epoch of Plant-lice," as applied to this period, far less whimsically inappropriate than it might at first sight seem to be.

After a brief sketch of the mode of life of these Plant-lice, or *Aphides*, as they are technically termed; of the structure of their singular piercing and sucking mouths; and of their relations to what are called "Blights;" the circumstances which have more particularly drawn the attention of naturalists to these insects were fully detailed.

It was between the years 1740 and 1750, in fact, that Bonnet, acting upon the suggestions of the illustrious Reaumur, isolated an *Aphis* immediately after its birth, and proved to demonstration, that not only was it capable of spontaneously bringing forth numerous living young, but that these and their descendants, to the ninth generation, preserved a similar faculty.

Observations so remarkable were not likely to pass unheeded; but notwithstanding the careful sifting which they have received, Bonnet's results have never been questioned. On the contrary, not only have Lyonet, Degeer, Kyber, Duvau, and others, borne ample testimony to their accuracy, but it has been shown that, under favourable conditions of temperature and food, there is practically no limit to this power of asexual multiplication, or as it has been conveniently termed, "Agamogenesis."

Thus Kyber bred the viviparous *Aphis Dianthi* and *Aphis Rosæ*

for three years in uninterrupted succession; and the males and true oviparous females of the *A. dianthi* have never yet been met with. The current notion that there is a fixed number of broods, "nine or eleven," is based on a mistake.

As, under moderately favourable conditions, an *Aphis* comes to maturity in about a fortnight; and as each *Aphis* is known to be capable of producing a hundred young, the number of the progeny which may eventually result even from a single *Aphis* during the six or seven warm months of the year is easily calculated. M. Tougard's estimate adopted (and acknowledged) by Morren, and copied from him by others, gives the number of the tenth brood as one quintillion. Supposing the weight of each *Aphis* to be no more than $\frac{1}{1000}$th of a grain, the mass of living matter in this brood would exceed that in the most thickly populated countries in the world.

The agamogenetic broods are either winged or wingless. The winged forms at times rise into the air, and are carried away by the wind in clouds; and these migrating hordes have been supposed to be males and females, swarming like the ants and bees! During the summer months it is unusual to meet other than viviparous *Aphides*, whether winged or wingless; but ordinarily, on the approach of cold weather, or even during warm weather, if the supplies of food fall short, the viviparous *Aphides* produce forms which are no longer viviparous, but are males and oviparous females. The former are sometimes winged, sometimes wingless. The latter, with a single doubtful exception, are always wingless.

The oviparous females lay their eggs, and then, like the males, die. It commonly happens also that the viviparous *Aphides* die, and then the eggs are left as the sole representatives of the species; but in mild winters many of the viviparous *Aphides* merely fall into a state of stupor and hybernate, to re-awake with the returning warmth of spring. At the same time the eggs are hatched and give rise to viviparous *Aphides*, which run through the same course as before. The species *Aphis*, therefore, is fully manifested not in any one being or animated form, but by a cycle of such, consisting of,—1st, the egg; 2nd, An indefinite succession of viviparous *Aphides*; 3rd, Males and females eventually produced by these, and giving rise to the egg again.

If, armed with the microscope and scalpel, we examine into the minute nature of these processes (without which inquiry all speculation upon their nature is vain), we find that the viviparous *Aphis* contains an organ similar to the ovarium of the oviparous female, in some respects, but differing from it, as Von Siebold was the first to show, in the absence of what are termed the colleterial glands and the spermatheca—organs of essential importance to the oviparous form.

In the terminal chambers of this "Pseud-ovarium," ovum-like bodies, thence called "pseud-ova," are found. These bodies pass one by one into the pseudovarian tubes, and there gradually become developed into young, living *Aphides*. As Morren has well said, therefore, the young *Aphides* are produced by "the individualization of a previously organized tissue."

The only organic operation with which this mode of development can be compared, is the process of budding or gemmation, as it takes place in the vegetable kingdom, in the lower forms of animal life, and in the process of formation of the limbs and other organs of the higher animals. And the parallel is complete if such a plant as the bulbiferous lily or the *Marchantia*, or such an animal as the *Hydra*, is made the term of comparison.

Thus agamogenesis in *Aphis* is a kind of internal budding or gemmation. If we inquire how this process differs from multiplication by true ova or "Gamogenesis," we find that the young ovum in the ovarium is also, to all intents and purposes, a bud, indistinguishable from the germ in the pseudovarium of the agamogenetic *Aphis*. Histologically there is no difference between the two; but there is an immense qualitative or physiological difference, which cannot be detected by the eye, but becomes at once obvious in the behaviour of the two germs after a certain period of their growth. Dating from this period, the pseudovum spontaneously passes into the form of an embryo, becoming larger and larger as it does so; but the ovum simply enlarges, accumulates nutritive matter, acquires its outer investments, and then falls into a state of apparent rest, from which it will never emerge, unless the influence of the spermatozoon have been brought to bear upon it.

That the vast physiological difference between the ovum and the pseudovum should reveal itself in the young state by no external sign, is no more wonderful than that primarily the tissue of the brain should be undistinguishable from that of the heart.

The phenomena which have been described were long supposed to be isolated, but numerous cases of a like kind, some even more remarkable, are now known.

Among the latter, the speaker cited the wonderful circumstances attending the production of the drones among bees, as described by Von Siebold; and he drew attention to the plant upon the table, *Cœlobogyne ilicifolia*, a female euphorbiaceous shrub, the male flowers of which have never yet been seen, and which nevertheless, for the last twenty years, has produced its annual crop of fertile seeds in Kew Gardens.

Not only can we find numerous cases of agamogenesis similar

to that exhibited by *Aphis* in the animal and vegetable worlds, but if we look closely into the matter, agamogenesis is found to pass by insensible gradations into the commonest phenomena of life. All life, in fact, is accompanied by incessant growth and metamorphosis; and every animal and plant above the very lowest attains its adult form by the development of a succession of buds. When these buds remain connected together, we do not distinguish the process as anything remarkable; when, on the other hand, they become detached and live independently, we have agamogenesis. Why some buds assume one form and some another, why some remain attached and some become detached, we know not. Such phenomena are for the present the ultimate facts of biological science; and as we cannot understand the simplest among them, it would seem useless, as yet, to seek for an explanation of the more complex.

Nevertheless, an explanation of agamogenesis in the *Aphis* and in like cases has been offered. It has been supposed to depend upon "the retention unchanged of some part of the primitive germ-mass;" this germ-mass being imagined to be the seat of a peculiar force, by virtue of which it gives rise to independent organisms.

There are however two objections to this hypothesis: in the first place, it is at direct variance with the results of observation; in the second, even if it were true, it does not help us to understand the phenomena. With regard to the former point, the hypothesis professes to be based upon only two direct observations, one upon *Aphis*, the other upon *Hydra;* and both these observations are erroneous, for in neither of these animals is any portion of the primitive germ-mass retained, as it is said to be, in that part which is the seat of agamogenesis.

But suppose the fact to be as the hypothesis requires; imagine that the terminal chamber of the pseudovarium is full of nothing but "unaltered germ-cells;" how does this explain the phenomena? Structures having quite as great claim to the title of "unaltered germ cells" lie in the extremities of the acini of the secreting glands, in the sub-epidermal tissues and elsewhere; why do not they give rise to young? Cells, less changed than those of the pseudovarium of *Aphis*, and more directly derived from the primitive germ-mass, underlie the epidermis of one's hand, nevertheless, no one feels any alarm lest a nascent wart should turn out to be an heir.

On the whole, it would seem better, when one is ignorant, to say so, and not to retard the progress of sound inquiry by inventing hypotheses involving the assumption of structures which have no existence, and of "forces" which, their laws being undetermined, are merely verbal entities.

XXXII

CONTRIBUTIONS TO THE ANATOMY OF THE BRACHIOPODA

Roy. Soc. Proc., vol. vii., 1854–55, *pp.* 106–117, 241–242

In the course of the dissection of certain Brachiopoda with which I have recently been engaged, I have met with so many peculiarities which are unnoticed in the extant and received accounts of their anatomy, that although the pressure of other duties prevents me from attempting to work out the subject with any degree of completeness for the present, I yet gladly avail myself of the opportunity of communicating a few of the more important results at which I have arrived, in the hope that they may find a place in the Proceedings of the Royal Society.

My investigations were principally made upon *Rhynchonella psittacea*, for specimens of which I am indebted to Prof. Edward Forbes, while Dr. Gray obligingly enabled me to compare them with *Waldheimia flavescens* and with *Lingula*.

1. *The Alimentary Canal of Terebratulidæ.*—Professor Owen, in both his earlier and his later memoirs on the anatomy of the Terebratulidæ, describes at length the manner in which the intestine, as he states, terminates on the right side between the lobes of the mantle.

On the other hand, Mr. Hancock has declared himself unable to observe at this point any such anal aperture, and concludes from his own observations that the latter is situated on the ventral surface of the animal in the middle line, just behind the insertion of the great adductor muscle. M. Gratiolet, in a late communication to the Académie des Sciences, takes the same view. To get rid of the obvious difficulty, that this spot is covered by the shell, and therefore that if the anus existed here, there would be no road of escape for

the fæces, Mr. Hancock and Mr. Woodward appear to be inclined to suppose that some cloacal aperture must exist in the neighbourhood of the pedicle.

The existence of any such aperture, however, has recently been denied with great justice by Professor Owen.

The result of my own repeated examinations of *Rhynchonella psittacea* and of *Waldheimia flavescens* is—1. that the intestine does not terminate on the right side of the mantle as Professor Owen describes it, but in the middle line, as Mr. Hancock describes it in *Waldheimia*, while in *Rhynchonella* it inclines, after curving upwards, to the *left* side; and 2. that there is no anus at all, the intestine terminating in a rounded cæcal extremity, which is straight and conical in *Waldheimia*, curved to the left side and enlarged in *Rhynchonella*.

I confess that this result, so exceptional in its character, caused me no small surprise, and I have taken very great pains to satisfy myself of the accuracy of my conclusion; but notwithstanding the strong prejudice to the contrary, to which the known relations of the anal aperture in *Lingula* gave rise, repeated observation has invariably confirmed it.

Professor Owen's statement is, that in *Rhynchonella* (*Terebratula*) *psittacea* "the intestine inclines to the right side and makes a slight bend forwards before perforating the circumscribing membrane in order to terminate between the mantle lobes on that side."—*On the Anatomy of the Brachiopoda*, p. 152.

I find, on the contrary (figs. 1 and 2), that the intestine passes at first straight downwards in the middle line, as in *Waldheimia*, but instead of terminating in a rounded tapering extremity as in that genus, it bends upwards and then curves round to the *left* side, forming a sort of free cæcum in the visceral cavity. My reasons for believing that it is a free cæcum are these:—in the first place, no anal aperture can be detected in the mantle cavity, either on the right or left sides, although the small size of the animal allows of its being readily examined uninjured, with considerable magnifying powers.

Secondly. If the shell be removed without injuring the animal and the visceral cavity be opened from behind by cutting through its walls close to the bulb of the pedicle, it is easy not only to see that the disposition of the extremity of the intestine is such as I have described it to be, but by gentle manipulation with a needle to convince oneself that it is perfectly unattached. And in connection with this evidence I may remark, that the tissues of the Brachiopods in general are anything but delicate; it would be quite impossible for instance

to break away the end of the intestine of *Lingula* from its attachments without considerable violence.

Thirdly. If the extremity of the intestine, either in *Rhynchonella* or in *Waldheimia*, be cut off and transferred to a glass plate, it may readily be examined microscopically with high powers, and it is then easily observable that its fibrous investment is a completely shut sac. In *Rhynchonella* the enlarged cæcum is often full of diatoma-

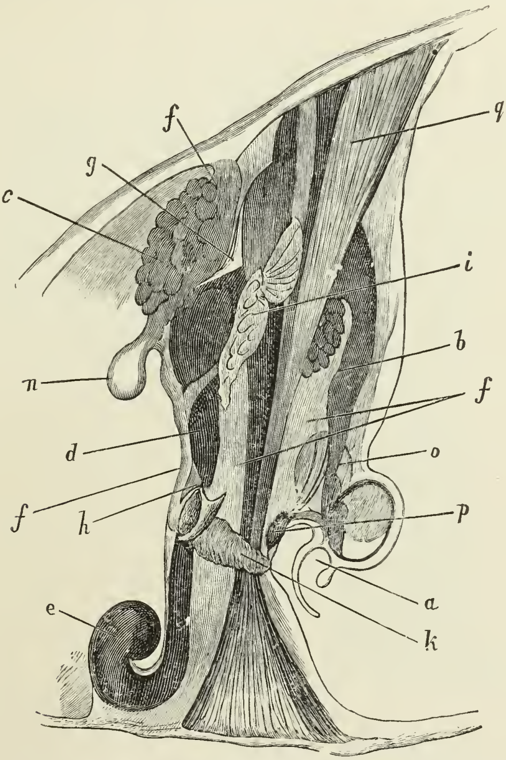


Fig. 1. *Rhynchonella psittacea*, viewed in profile; the lobes of the mantle and the pedicle being omitted.

a. mouth; *b.* œsophagus; *c.* stomach and liver; *d.* intestine; *e.* imperforate rectum; *f.* mesentery; *g.* gastro-parietal bands; *h.* ilio-parietal bands; *i.* superior 'heart'; *k.* inferior 'heart'; *l.* genital bands; *m.* openings of pallial sinuses; *n.* pyriform vesicle; *o.* sac at the base of the arm; *p.* ganglion; *q.* adductors.

ceous shells, but it is impossible to force them out at its end, while if any aperture existed they would of course be readily so extruded.

However anomalous, physiologically, then, this cæcal termination of the intestine in a molluscous genus may be, I see no way of escaping from the conclusion that in the *Terebratulidæ* (at any rate in these two species) it really obtains. There are other peculiarities

about the arrangement of the alimentary canal, however, of which I can find either no account at all or a very imperfect notice.

The intestinal canal (figs. 1 and 2 *b*, *d*, *e*) has an inner, epithelial, and an outer fibrous coat ; the latter expands in the middle line into a sort of mesentery, which extends from the anterior face of the intestine between the adductors, to the anterior wall of the visceral chamber, and from the upper face of the intestine to the roof of the

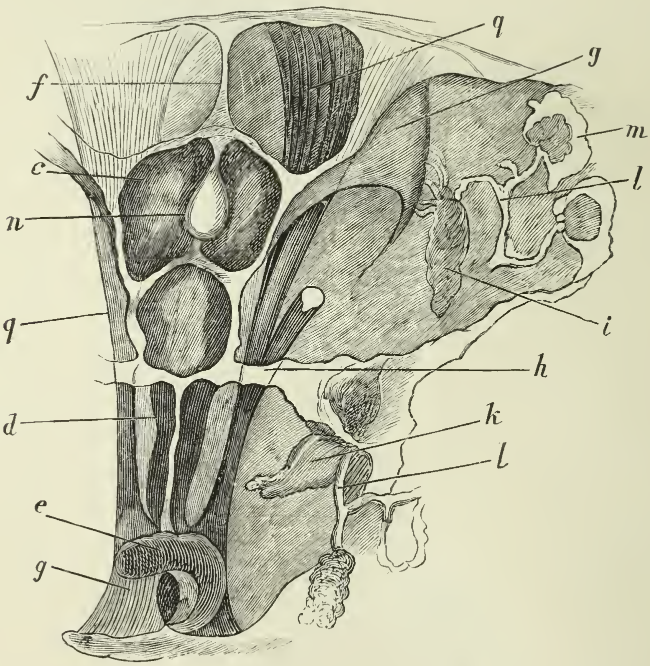


Fig. 2. The same viewed from behind, the pedicle having been cut away. The left half of the body and the liver are omitted. (For explanation see under Fig. 1.)

visceral chamber ; while posteriorly it extends beyond the intestine as a more or less extensive free edge. I will call this the *mesentery* (*f*).

From each side of the intestinal canal, again, the fibrous coat gives off two ' bands,' an upper (*g*), which stretches from the parietes of the stomach to the upper part of the walls of the visceral chamber, forming a sort of little sheath for the base of the posterior division of the adductor muscle, which I will call the *gastro-parietal band* ; and a lower, which passes from the middle of the intestine to the parietes, supporting the so-called '*auricle*.' I will call this the *ilio-parietal* band (*h*).

The ilio-parietal and gastro-parietal bands are united by certain

other ridges upon the fibrous coat of the intestine, from whose point of union in the middle line of the stomach posteriorly, a pyriform vesicle (*n*) depends.

The mesentery divides the liver into two lateral lobes, while the gastro-parietal bands give rise to the appearance that these are again divided into two lobules, one above the other. I am inclined to think that these bands are what have been described as 'hepatic arteries,' at least there is nothing else that could possibly be confounded with an arterial ramification upon the liver.

This description applies more especially to *Rhynchonella* and *Waldheimia*, but the arrangement in *Lingula* is not essentially different.

2. *The Circulatory System of Terebratulidæ.*—Considerable differences of opinion have prevailed among comparative anatomists as to the nature and arrangement of the vascular system in the Brachiopoda. A pair of organs, one on each side of the body, have been recognized as Hearts since the time of Cuvier, who declared these hearts in *Lingula* to be aortic, receiving the blood from the mantle and pouring it into the body, the principal arterial trunks being distributed into that glandular mass which Cuvier called ovary, but which is now known to be the genital gland of either sex.

Professor Owen in his first memoir follows Cuvier's interpretation, stating that in *Orbicula* the pallial veins terminate in the hearts, from which arterial branches proceed to the liver and ovary. Professor Owen further adds for the Brachiopoda in general,—

" Each heart, for example, in the Brachiopoda is as simple as in Ascidia, consisting of a single elongated cavity, and not composed of a distinct auricle and ventricle as in the ordinary Bivalves," and he compares the hearts of Brachiopoda to the auricles of Arca, &c. (Trans. Zoological Society, vol. i. p. 159).

In 1843, however, M. Vogt's elaborate memoir on *Lingula* appeared, in which the true complex structure of the 'heart' in this genus was first explained and the plaited 'auricle' discriminated from the 'ventricle ;' and in 1845, Professor Owen, having apparently been thus led to re-examine the circulatory organs of Brachiopoda, published his 'Lettre sur l'appareil de la Circulation chez les Mollusques de la Classe des Brachiopodes,' in which he felicitates M. Milne-Edwards on the important confirmation of the views which the latter entertains with respect to the lacunar nature of the circulation in the Mollusca, afforded by the Brachiopoda, and describes each heart of the Terebratulidæ as consisting of a ventricle and a plaited auricle, the pallial veins not terminating in the latter but in the general visceral cavity. As the Professor does not recall the view-

which he had already taken of the circulation in *Orbicula*, I presume that he considers two opposite types of the circulatory organs to obtain in the Brachiopoda, the direction of the current being from the mantle through the heart towards the body in *Orbicula*, and from the mantle through the body towards the heart in *Terebratula*.

The possibilities of nature are so various that I would not venture, without having carefully dissected *Orbicula*,—no opportunity of doing which has yet presented itself,—to call this view in question, but I think it seems somewhat improbable. Indeed the structural relations which I have observed and which are described below, do not appear to me to square with any of the received doctrines of Brachiopod circulation, but I offer them simply as facts, not being prepared at present to present any safe theory on the subject.

In *Waldheimia flavescens* there are two 'hearts,' situated as Professor Owen describes them, but so far as I have been able to observe, the ventricle cannot be described as an 'oval' cavity, inasmuch as it is an elongated cavity bent sharply upon itself. Hastily examined of course this may appear oval. I have been similarly unable to discover 'the delicate membrane of the venous sinuses,' which is said by Professor Owen to "communicate with and close the basal apertures of the auricles," or to perceive that the auricular cavity can be "correctly described as a closed one, consisting at the half next the ventricle, of a beautifully plicated muscular coat in addition to the membranous one, but at the other half next the venous sinus of venous membrane only; the latter might be termed the auricular sinus, the former the auricle proper."

I presume that 'this delicate membrane of the venous sinuses' is what I have called the ilio-parietal band, in which the base of the auricle is as it were set, like a landing-net in its hoop, but this does *not* close the base of the auricle, the latter opening widely into the visceral chamber.

I have equally failed in detecting any arteries continued from the apices of the ventricles; and I have the less hesitation in supposing I have not overlooked them, as Mr. Albany Hancock, whose works are sufficient evidence of the value of his testimony, permits me to say that he long since arrived at the conclusion that no such arteries exist.

What has given rise to the notion of the existence of these arteries appears to me to be this. A narrow band resembling those I have already described, is attached in *Waldheimia* along the base of the 'ventricle' and the contiguous outer parietes of the auricle: inferiorly it passes outwards to the sinuses, and running along their inner

wall, forms a sort of ridge or axis[1] from which the genitalia, whether ovaria or testes, are developed, stretching through their whole length and following the ramifications of the sinuses. It is the base of these ridges seen through the walls of these sinuses, where they extend beyond the genitalia, which have been described as arteries.

The upper end of the band passes into the sinuses of the upper lobe of the mantle, and comes into the same relation with the genitalia which they enclose.

The walls of the auricle in *Waldheimia* are curiously plaited, but I have been unable, in either auricle or ventricle, to detect any such arrangement of muscular fibres as that which has been described. The epithelial investment of the auricle, on the other hand, is well developed, and in the ventricle the corresponding inner coat is raised up into rounded villous eminences.

The ventricle lies in the thickness of the parietes, while the auricle floats in the visceral cavity, supported only by the ilio-parietal band. The former is at first directed downwards, but then bends sharply round and passes upwards to terminate by a truncated extremity close to the subœsophageal ganglion and bases of the arms.

Mr. Hancock informs me, that in his dissections he repeatedly found an aperture by which the apex of the 'ventricle' communicated with the pallial cavity; and that, taking this fact in combination with the absence of any arteries leading from this part, he had been tempted to doubt the cardiac nature of these organs altogether, and to regard them rather as connected with the efferent genital system, had not the difficulty of determining whether these apertures were artificial or natural prevented his coming to any definite conclusion at all.

Before becoming acquainted with Mr. Hancock's investigations, I had repeatedly observed these apertures in *Rhynchonella*, but preoccupied with the received views on the subject, I at once interpreted them as artificial. A knowledge of Mr. Hancock's views, however, led me to reconsider the question, and I have now so repeatedly observed these apertures both in *Waldheimia* and in *Rhynchonella*, that I am strongly inclined to think they may after all be natural.

If these organs be hearts, in fact, *Rhynchonella* is the most remarkable of living Mollusks, for it possesses *four* of them. Two of these occupy the same position as in *Waldheimia*, close to the origins of the calcareous crus (*k*), while the other two are placed above these, and

[1] This arrangement is, I find, particularly described by M. Gratiolet.

above the mouth, one on each side of the liver (*i*). It is these latter which Professor Owen describes, while he has apparently overlooked the other two, at least he says (speaking as I presume of *Rhynchonella*) (*l. c.* p. 148) that the venous sinuses "enter the two hearts or dilated sinuses which are situated exterior to the liver, and in *T. Chilensis* and *T. Sowerbii* just within the origins of the internal calcareous loop."

The fact is, that while the ilio-parietal bands support two 'hearts' as usual, the gastro-parietal bands are in relation with two others. The base of the 'auricle' of the latter opens into the re-entering angle formed by the gastro-parietal band with the parietes, while its apex is directed backwards to join the ventricle, which passes downwards and backwards along the posterior edge of the posterior division of the adductor muscle.

The auricles in *Rhynchonella* are far smaller, both actually and proportionally, than in *Waldheimia.* They exhibit only a few longitudinal folds, and not only present the same deficiency of muscular fibres as those of *Waldheimia*, but are so tied by the bands which support them that it is difficult to conceive how muscular fibres, even if they existed, could act. The 'ventricles' in like manner lie obliquely in the parietes of the body, and simply present villous eminences on their inner surface, which has a yellowish colour.

All these 'hearts' exhibit the same curious relation with the genitalia in *Rhynchonella* as in *Waldheimia*; that is to say, a 'genital band' (*l*) proceeds from the base of the 'ventricle' and becomes the axis of the curiously reticulated genital organ. But in *Rhynchonella* the genital bands of the upper genitalia come from their own 'hearts.'

The arrangement of the genitalia in *Rhynchonella* is very remarkable. The sinuses have the same arrangement in each lobe of the mantle. The single trunk formed by the union of the principal branches in each lobe opens into the inner and anterior angle of a large semilunar sinus which surrounds the bases of the adductors, and opens into the visceral cavity. The floor of this great sinus is marked out into meshes by the reticulated genital band, and from the centre of each mesh a flat partition passes, uniting the two walls of the sinus, and breaking it up into irregular partial channels.

There are the same anastomosing bands uniting the gastro-parietal and ilio-parietal bands on the stomach in *Rhynchonella* as in *Waldheimia*, and a pyriform vesicle of the same nature,

but I did not observe in *Rhynchonella* those accessory vesicles upon the origins of genital bands, which I observed once or twice in *Waldheimia.*

I could find no trace of arteries terminating the elongated, ovoid and nearly straight 'ventricles' of *Rhynchonella*; their ends appeared truncated, and as I have already said, repeatedly presented a distinct external aperture.

Such appear to me to be the facts respecting the structure of the so-called hearts in the *Terebratulidæ*; what I believe to be an important part of their peripheral circulatory system, has not hitherto so far as I am aware, received any notice.

In *Waldheimia* the membranous walls of the body, the parieto-intestinal bands and the mantle, present a very peculiar structure; they consist of an outer and an inner epithelial layer, of two corresponding fibrous layers, and between them of a reticulated tissue, which makes up the principal thickness of the layer, and in which the nerves and great sinuses are imbedded.

The trabeculæ of this reticulated tissue contain granules and cell-like bodies, and I imagined them at first to represent a fibro-cellular network, the interspaces of which I conceived were very probably sinuses. Sheaths of this tissue were particularly conspicuous along the nerves. On examining the arms, however, I found that the oblique markings, which have given rise to the supposition that they are surrounded by muscular bands, proceeded from trabeculæ of a similar structure, which took a curved course from a canal which lies at the base of the cirri (not the great canal of the arms, of course) round the outer convexity of the arm, and terminated by breaking up into a network. These trabeculæ, however, were not solid but hollow, and the interspaces between them were solid. The network into which they broke up was formed by distinct canals, and then, after uniting with two or three straight narrow canals which ran along the outer convexity of the arm close to its junction with the interbrachial fold, appeared to become connected with a similar system of reticulated canals which occupied the thickness of that fold.

It was the examination of the interbrachial fold, in fact, which first convinced me that these reticulated trabeculæ were canals; for it is perfectly clear that vessels or channels of some kind must supply the proportionally enormous mass of the united arms with their nutritive material, and it is so easy to make thin sections of this part, that I can say quite definitely that no other system of canals than these exists in this locality.

The *facts*, then, with regard to the real or supposed circulatory organs of the *Terebratulidæ*, are simply these :—

1. There are two or four organs (hearts), composed each of a free funnel-shaped portion with plaited walls, opening widely into the visceral cavity at one end, and at the other connected by a constricted neck, with narrower, oval or bent, flattened cavities, engaged in the substance of the parietes. The existence of muscular fibres in either of these is very doubtful. It is certain that no arteries are derived from the apex of the so-called ventricle, but whether this naturally opens externally or not is a point yet to be decided.

2. There is a system of ramified peripheral vessels.

3. There are one or more pyriform vesicles.

4. There are the large 'sinuses' of the mantle, and the 'visceral cavity' into which they open.

To determine in what way these parts are connected and what functions should be ascribed to each, it appears to me that much further research is required.

Nervous System of Terebratulidæ.—Professor Owen describes and figures the central part of this system as a ring surrounding the oral aperture, its inferior portion being constituted by a mere commissural band.

M. Gratiolet, however, states with justice that the inferior side of this collar is the thicker, and I find both in *Rhynchonella* and in *Waldheimia* that it constitutes, in fact, a distinct oblong ganglion, of a brownish colour by reflected light. From its extremities commissural branches pass round the mouth, while other cords are distributed to the arms, to the superior and inferior pallial lobes, and to the so-called hearts. The nerves are marked by fine and distinct longitudinal striations, and can be traced to the margins of the pallial lobes, where they become lost among the muscular fibres of the free edges of the mantle.

Structure of the Arms.—I have not been able to convince myself of the existence of that spiral arrangement of the muscular fibres of the arms which has been described in *Rhynchonella* and *Waldheimia.* I have found the wall of the hollow cylinder of the arm to be constituted (1) externally, by an epithelium, within which lie (2) the reticulated canals, which have been already described ; (3) by a delicate layer of longitudinal or more oblique and transverse fibres, which are probably muscular, and (4) internally by a granular epithelial layer.

In *Rhynchonella* the bases of the arms are terminated by two considerable sacs, which project upwards into the visceral cavity. Have

these the function of distending and so straightening the spirally coiled, very flexible arms of this species?

Affinities of the Brachiopoda.—All that I have seen of the structure of these animals leads me to appreciate more and more highly the value of Mr. Hancock's suggestion, that the affinities of the Brachiopoda are with the Polyzoa. As in the Polyzoa, the flexure of the intestine is neural, and they take a very natural position among the neural mollusks between the Polyzoa on the one hand, and the Lamellibranchs and Pteropoda on the other.

The arms of the Brachiopoda may be compared with those of the Lophophore Polyzoa, and if it turns out that the so-called hearts are not such organs, one difference will be removed.

In conclusion, I may repeat what I have elsewhere adverted to, that though the difference between the cell of a Polyzoon and the shell of a Terebratula appears wide enough, yet the resemblance between the latter with its muscles and the Avicularium of a Polyzoon, is exceedingly close and striking.

My attention having been called within the last two or three days, to an error in my paper on the Anatomy of the Brachiopoda, published in No. 5 of the Royal Society's Proceedings, I beg to be allowed to take the earliest opportunity of correcting it. At p. 111 of that paper the following paragraph will be found:—

"In 1843, however, M. Vogt's elaborate Memoir on *Lingula* appeared, in which the true complex structure of the 'heart' in this genus was first explained and the plaited 'auricle' discriminated from the 'ventricle;' and in 1845, Professor Owen, having apparently been thus led to re-examine the circulatory organs of the Brachiopoda," &c. &c.

Now, in point of fact, though M. Vogt *does* describe and accurately figure the structures called 'auricle' and 'ventricle' in *Lingula*[1], yet he has not only entirely omitted to perceive their connection, or to indicate the 'auricular' nature of the former, but he expressly states that the so-called 'hearts' are "simple, delicate, pyriform sacs" (p. 13).

I presume that my recollection of M. Vogt's figures was more vivid than that of his text; for having been unable, notwithstanding repeated endeavours, to re-obtain the memoir when writing my paper,

[1] Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften. Band VII.

I felt justified in trusting to what seemed my very distinct recollection of its sense. I had the less hesitation in doing this, as in M. Vogt's subsequently published 'Zoologische Briefe[1],' he gives the received interpretation to the parts of the so-called 'hearts' without any indication of a change of opinion.

I make this statement in explanation of what might otherwise seem to be great carelessness on my part, and for the purpose of further pointing out that M. Vogt not having made the supposed discovery, it is quite impossible that Professor Owen's researches should have been suggested by it.

[1] Frankfort, 1851, vol. i. p. 285.

XXXIII

ON A HERMAPHRODITE AND FISSIPAROUS SPECIES OF TUBICOLAR ANNELID

Edinb. New Phil. Journ., vol. i., 1855, *pp.* 113–129

In the course of a series of dredging operations, in which I have lately been engaged, upon the shores of Caermarthen Bay, in the neighbourhood of Tenby, I took, upon one occasion and in one locality (in about six fathoms water, near Proud Giltar), the Annelid which is the subject of the present communication. It is questionable, however, whether the animal is so rare as I might have been led to suppose from this solitary instance of its occurrence within my own knowledge—for I had afterwards the opportunity of seeing masses of its calcareous habitation considerably larger than that which I took myself, in the celebrated collection of the late Mr. Lyons of Tenby.

The *Vermidom* (as one might conveniently term the habitations of tubicolar annelids in general) of this annelid is composed of very fine, more or less undulated, white, calcareous tubes, attached by one end to some solid body. Rising from this fixed base, they unite together side by side into irregular bundles, and these bundles anastomose like bundles of nerves in their plexuses—leaving irregular spaces here and there, and thus forming a kind of coarse solid network (fig. 1). Each tube has a circular section, but can hardly be called cylindrical, because it is thickened at intervals, so as to be obscurely annulated.

When placed in a vessel of clear sea-water, the annelids issue from the tubules of their vermidom, and each spreading out its eight branchial filaments and displaying its bright red cephalic extremity—the mass assumes a very beautiful and striking appearance—singularly resembling a tubuliparous polyzoarium (fig. 2).

If, however, a portion of the calcareous mass be broken down, and its delicate fabricators carefully extracted (fig. 3), their annelidan nature becomes immediately obvious ; and in determining the exact place of this form among the tubicola, the expanded membrane which fringes the sides of the body, the peculiar branchial plumes, and the absence of any operculum, would point at once to the genus *Protula*[1] as that to which this species belongs, were it not for two most remarkable peculiarities of its organization, which, so far as we know at present, are to be found in no *Protula ;* and one of them in no other tubicolar annelid.

These peculiarities are, in the first place, that this species undergoes *fissiparous multiplication ;* and, in the second, that it is *hermaphrodite*—the male and female reproductive elements being, unequivocally, developed in the same individual.

So far as I am aware, the process of fissiparous multiplication has hitherto been observed in only one family among the errant annelids, the *Syllidea* (of Grube) ; in only one family among the *Scoleidæ* (*Hirudinidæ* and *Lumbricidæ*), that of the *Naidea*,—and in only one genus among the tubicolar annelids, *Filograna.*

Hermaphrodism has hitherto been observed in no errant or tubicolar annelid.[2] Indeed the author to whom we are indebted for the most beautiful researches into annelid organization extant, M. de Quatrefages, thus concludes his elaborate memoir on the nervous system of the annelida :—

"We must then seek elsewhere (than in the nervous system) the characteristics on which to base the divisions which are necessitated by the great extent of this group, and the multiplicity of types which it embraces. Now, as an anatomical character, there is nothing more distinct and well marked than the union or separation of the sexes in the same individual. These differences of organization, besides, indicate profound physiological distinctions, which have long been justly appreciated by botanists. I am, therefore, more and more inclined to believe that the distinction of the annelids (Vers) into monœcious and diœcious ought to be adopted in science." [3]

In arriving at this conclusion, M. de Quatrefages was, of course,

[1] On consulting the original description of *Filograna*—a genus to which the form of the Vermidom of this species would at first induce one to refer it, its affinities therewith appear evident ; but whether there is any real difference between Filograna and Protula is a question for further consideration.

[2] See among other authorities, Frey and Leuckart, *op. cit. inf.*, p. 87, who examined Hermella, Vermilia, Fabricia, and Spirorbis, among the tubicolar annelids, with especial reference to this point.

[3] Types inférieurs de l'Embranchement des Annelés. Ann. des Sc. Nat. 1850.

only furnishing additional evidence for the justice of that division of the annelids into the *Annélides* proper, characterized by the separation of their sexes—and the *Scoléides*, characterized by their hermaphrodism—which was first established by M. Milne-Edwards, and which has been very generally received.

However, on a careful survey of the whole class of worms, many facts come to light which throw considerable doubt on the propriety of raising unisexuality or hermaphrodism into distinctive characters of large groups. We have hermaphrodite *Rotifera*, and unisexual *Rotifera*. The *Nemertidæ* and *Microstomum* are unisexual, the other *Turbellaria* hermaphrodite; there appears to be considerable doubt as to the universality of hermaphrodism in the *Trematoda* even; and *Echinorhynchus*, which cannot be placed very far from the *Tæniadæ* and *Distomata*, is well known to be unisexual, and there is therefore, perhaps, nothing so very anomalous in the discovery of a truly hermaphrodite tubicolar annelid. It is another question how far it need affect the classification to which I have alluded.

The fluctuation in the terminology of the classification of the annelids, in fact, has proceeded from the very common but always obstructive practice of giving notional instead of trivial names to incomplete groups of animals. Cuvier divided the annelids into errant, tubicolar, terricolar, &c., deriving his terminology from the habits of those with which naturalists were then acquainted; but, with the advance of knowledge, it was found that some of the *Errantia* inhabit tubes, while one main division of the "*Terricola*" consists of aquatic worms; and thus these notional terms, instead of aiding the memory as they were intended to do, served simply to originate and propagate erroneous conceptions. There can be no doubt that the divisions established by Cuvier are essentially natural, and had he devised some happily unintelligible Grecism, instead of the names which he actually adopted, they would have stood, their definitions altering with the progress of knowledge, until this day.

The divisions proposed by M. Milne-Edwards possess exactly the qualification which is here wanting. *Annélides* and *Scoléides* may mean anything, and, as names of groups, may very conveniently remain, even if it should be found necessary to remodel the whole definition which was primarily assigned to them. It appears to me, therefore, that if the statements which follow be confirmed, they will lead, not to an alteration or sub-division of the group of *Annelides*, but to a widening of its definition so as to include hermaphrodite forms; or perhaps it would be better to admit that owing to the imperfection of our knowledge, we have not yet a *definition* of either

Annélides or *Scoléides* at all, but that we must arrange under the former head all those worms which resemble the errant and tubicolar sea worms more than anything else, while those which resemble the land and fresh water worms must fall under the latter category. If, from the great division of the *Annulosa*, we take away those animals which are characterized by the possession of one or more of the following characters—1. Articulated appendages. 2. Such appendages modified into jaws around the mouth. 3. A true heart in communication with the perivisceral cavity: that is, the Insecta, Myriapoda, Arachnida, and Crustacea—we have left a large division of the animal kingdom, to which the old term of *Vermes* might well be appropriated, had it not been already used in so many significations. For this division, whose members are united by a marked community of structure and development, and which includes the *Annelida* of Cuvier and a large section of his *Radiata*, viz., the *Entozoa*, the *Rotifera*, and the *Echinodermata*, I have elsewhere proposed the name of *Annuloida*, a term parallel to that very useful one of *Molluscoida* (*Molluscoides*), invented by Milne-Edwards for the *Polyzoa* and *Ascidians*.[1]

If it be remembered that it is only within the last few years that the structure and development of these *Annuloida*—which present extraordinary difficulties to the investigator—have been made the subjects of thorough and complete examination, it will not be a matter of surprise that, at present, the subordinate division of the group must be effected more by reference to types than by exact definition. Of course this is still more the case with the smaller sub-divisions; and until much more light has been thrown on these most interesting but most perplexing creatures, I think it would be well to understand the existing classes and orders to be purely conventional and artificial. For my own part, I doubt greatly whether any well-marked natural demarcation can, at present, be drawn between the *Annelida* (M. E.) and the *Scoleidæ*, or between these and the *Entozoa*; or, again, between the latter, the *Turbellaria*, and the *Rotifera*; or, once more, between the *Annelida* and the *Echinodermata*; though I have little doubt that the progress of inquiry will tend here, as elsewhere, to eliminate osculant forms, and to substitute definitions for types.

Not only does it appear to me that, under these circumstances, it

[1] In writing this passage it escaped my memory that the very same division had been long ago proposed by Milne-Edwards himself:

"Je crois qui'l faudrait diviser cet embranchement (Les Articulés) en deux groupes principaux, l'un les articulés a pieds articulés, et l'autre les annèlides, les Helminthes, les Rotateurs, &c., serie à laquelle on pourrait donner le nom vulgaire des Vers." Sur la Circulation dans les Annèlides. Ann. des Sc. Nat., 1838, p. 194.

is inexpedient to create new sectional terms ; but until a more extended and careful examination of the tubicolar annelides shall have been made with reference to these very points, I do not think it is worth while even to found a new genus for the form I am about to describe, as it possesses all the essential characters of *Protula*. Specifically, however, it appears to be distinct from all forms of *Protula* hitherto described, and I therefore propose to call it *Protula Dysteri*, after my friend Mr. Dyster of Tenby, in whose society it was discovered, and from whom I hope some day to see good work in this branch of science.

I have already described the vermidom of this species, and I now therefore pass to the details of the organization of the animal itself. *Protula Dysteri* (fig. 3) possesses a very elongated body, which may be conveniently divided into a cephalic, a thoracic, an abdominal, and a caudal portion.

The cephalic portion (fig. 3, *e*) can hardly be said to constitute a distinct head, for the oral aperture, which is wide and funnel-shaped, is terminal. The dorsal margin of the oral aperture is formed by a prominent rounded lobe, beneath which are two richly-ciliated, short filaments, which adhere to the base of the branchial plumes, and might be regarded either as their lowest pinnules, or perhaps, more properly, as tentacles analogous to the operculigerous tentacles of the Serpulæ. On the ventral side the margin is deeply incised, so that a rounded fissure, bounded by two lips, lies beneath and leads into the oral cavity. From each side of the head springs a distinct branchial plume, whose peduncle immediately divides into four branches. These are beset with a double series of short filiform pinnules, the origins of each series alternating with those of the other. The termination of each branch is somewhat clavate, and when expanded the eight branches are usually gracefully incurved towards one another, the whole having not a little the aspect of a Comatula.[1]

The thoracic portion of the body (fig. 3, *e f*) is short, but wide and somewhat flattened. It is produced laterally into nine pairs of close-set, double pedal processes. The lower portion of each process forms a mere transverse ridge, beset with the peculiar hooks to be described by and by ; the upper process, on the other hand, is conical, and is provided with elongated setæ. The most striking feature of the thorax, however, consists in the peculiar membranous expansion, (*b*) which, arising as a ridge upon each side of what might be termed the nuchal surface of the animal, and attached to the sides of the thorax,

[1] It is worthy of note, how very crinoid the branchial plumes would be if their skeleton were calcified instead of simply cartilaginous.

above the bases of the feet, runs down to terminate on the ventral surface, behind the last pair of thoracic appendages. From this origin it extends as a wide free membrane beyond the setæ, forming an elegant collar around the head, on whose ventral surface the expansions of each side unite, and form a wide reflexed lobe (fig. 4, *g*), while posteriorly they remain separate. To the thorax succeeds what may be called the abdomen, which is much longer than the other regions of the body; and is, besides, distinguished from them by the imperfect development of the feet, and the paucity of the setæ and hooks. In this, and in the caudal portion of the body, the relative position of the hooks and setæ is the reverse of what it is in the thorax, the former being superior, and the latter inferior.[1]

The caudal portion of the body is short, and wider than the abdomen. Its rings are close-set, with well-developed hooks and setæ, and it is terminated by two conical papillæ between which the anus is situated. There are not less than 50 rings in the whole body. Cilia could be detected in active motion on many parts of the external surface, on the bases of the feet, on the rudimental tentacles, and scattered in tufts over the whole surface of the thoracic expansions.

Having thus sketched its external character, I will now pass to the minuter features presented by the organization of the animal.

Branchial plumes.—The principal mass of these organs is formed by a clear, firm, supporting axis, so marked transversely as very closely to resemble the *chorda* of an *Amphioxus*. The lower end of this axis terminates by a somewhat pointed extremity, which lies in immediate proximity to the œsophagus (fig. 4), and receives the insertion of the lateral longitudinal muscles of the body. Superiorly, as has already been said, the axis divides into four branches, one of which enters the stem of each branchia and forms its skeleton and support, sending lateral processes into each of the pinnules. These, however, are much more delicate, and are composed of oblong particles set end to end; somewhat like the axis of the tail of an Ascidian larva. All this branchial skeleton, as one might term it, is invested by a continuation of the general parietes of the body, which adheres closely to the outer side of the stem and pinnules, but leaves a space on their inner side. In this space lies the so-called "blood"-vessel, with its green contents. It does not fill the space, but lies

[1] According to Grube, this is the case in all the Serpulacea. See his most excellent work—"Die Familien der Anneliden." 1851.

loosely in it; the interval between it and the walls of the filament being, I suppose, in continuity with the perivisceral cavity.[1]

The whole of the internal surface of the branchiæ is provided with long, close-set, vibratile cilia, while nothing of the sort is visible externally. The end of the stem has a very peculiar structure. It is somewhat enlarged by the development within its walls of a number of elongated granular masses of about $\frac{1}{1000}$ inch in length, entirely made up of very minute, strongly refracting granules, which, when pressed out, become rapidly diffused and dissolved in the surrounding water. These bodies were not confined to the ends of the branchial stems, but similar aggregations existed at the ends of many of the pinnules, and were also very regularly developed in little elevations seated upon the sides of the stem in front of the base of each pinnule.[2]

Alimentary Canal.—The œsophagus leads into a pyriform, more or less marked, dilatation or crop, provided with thicker walls than the remainder of the alimentary canal (fig. 5). The crop communicates by a constricted portion with a wide stomach, whose walls are strongly tinged by deep brown granules. This passes into a narrow intestine, which widens in the caudal region into a sort of rectum, opening externally, between the terminal papillæ, by a richly-ciliated anus.

In every segment the intestine was united to the parietes by delicate transverse membranous dissepiments, forming partitions across the perivisceral cavity, and thus dividing it into a series of chambers, which, so far as I could observe, did not communicate with one another, though it would be unsafe absolutely to affirm this.

"*Vascular*" *System.* — The so-called "blood"-vessels[3] of the

[1] The skeleton of the branchiæ of the Serpulacea has been well and carefully described by De Quatrefages in his valuable memoir "Sur la Circulation des Annelides," Annales de Sciences Naturelles, 1850; and that of Sabella unispira by Grube, so long ago as 1838. See his memoirs "Zur Anat. und Physiologie der Kiemenwurmer." 1838.

[2] Are the peculiar rounded whitish granular patches which occupy a similar position on the arms of Comatula of a corresponding nature, or are these really testes? I have never been able to find developed spermatozoa in them, nor anywhere else in Comatula.

[3] At the last meeting of the British Association (September 1854), I ventured to propound the theory that what are commonly called the blood-vessels of the Annelida are not "blood"-vessels at all; that is, that these vessels, and the fluid which they contain, are not the homologues of the blood-vessels and blood of Vertebrata, Mollusca, and Articulata, the latter being represented in annelids by the perivisceral cavity and its contained fluid, whose anatomical and physiological importance have been so excellently and exhaustively developed by De Quatrefages. See his researches on the Annelids, and more particularly his memoir "Sur la cavité generale du corps des Invertebrès." It is to be hoped that M. de Quatrefages understands that instructed Englishmen do not countenance the unwarrantable attempts that have been made to depreciate his merits in this country.

Annelida were represented, in the present case, by lateral contractile vessels which ran upon each side of the intestine, and gave off transverse branches on to the dissepiments, from which twigs proceeded dorsally and ventrally.

The dimensions of these lateral vessels varied considerably; sometimes they were comparatively narrow, but in other instances so wide as to appear to form a complete sheath around the intestine. They contained a deep green, clear fluid, totally without corpuscles or solid elements of any kind, while they themselves, when empty, were usually quite colourless; but I would draw attention to the curious fact, which I have also observed in other annelids, that in the anterior part of their course they occasionally present bright green, granular particles, imbedded in, and adhering to, their outer surface.

The opacity of the anterior end of the animal, resulting from the quantity of deep red pigment, prevented any very certain observation of the manner in which these vessels terminate there. I am inclined to think, however, that they open into a circular vessel, from which the branchial vessels arise.

It was no less difficult, in an adult specimen, to determine whether a ventral vessel existed or not; but in a young form, I saw such a vessel communicating with the inferior transverse branches, and distinctly contracting. It was superficial to the ciliated canal immediately to be described.

Of a dorsal vessel I could find no trace. The final ramuscules of the superior transverse branches of the lateral trunks were found, whenever they could be distinctly observed, to terminate *cæcally*. There could be no question whatever, that these cæcal ends were the natural terminations of the ramuscules, as the animal under observation had been subjected to no violence, and was viewed by transmitted light. I am the more particular in insisting upon this point, as one might very readily be led, in dissecting annelids, to suppose that cæcal terminations of the vessels are much more frequent than they really are. Their vessels, in fact, possess, in a very high degree, that tendency to contract when torn, which is so well known in the arteries of the higher animals. And if under the simple microscope the vessels of an Eunice or Nereid be deliberately pulled asunder, it is most curious to observe how very little of the contained fluid pours out, and how smooth and round the torn ends immediately become. In our *Protula*, however, the mode of examination was such as to preclude all chance of error from this source; and I have

besides fully confirmed the fact that this mode of termination,[1] in the singular and beautiful genus *Chlorœma*, which has the advantage of great transparency. In this animal it is easy to observe that though many of the ultimate branches of the vessels anastomose, and thus give rise to a network, yet that there are also many branches of no inconsiderable dimensions, which terminate in cæcal extremities. Such vessels may be frequently observed coming off from the transverse trunk and hanging freely into the perivisceral cavity, attached only by a few delicate threads of connective tissue, to the parietes. It is most curious to watch the regular contractions of these pendent vessels, their momentary emptying, and their subsequent distention and erection by the returning wave of fluid. And in considering the nature of this remarkable system of vessels, it is most important to note that we have here, at any rate, no circulation, but a mere backward and forward undulation.[2]

Ciliated Canal.—A clear, longitudinal, very narrow ($\frac{1}{1400}$ to $\frac{1}{3300}$ inch) canal (fig. 6, *a*) may be observed extending along the ventral surface of the intestine in the middle line, from the anus, where it appeared to me to open, as far as the brown dilated stomach, when it either stopped or became so obscured as to be no further traceable. The canal had well-marked walls with a double contour, which sometimes appeared curiously broken ; and contained, set along its dorsal wall, one to four longitudinal series of cilia (fig. 9). These were placed at regular intervals, and worked together, as if they were pulled by a common string. In young specimens there was only one cilium in each row, but in the older ones I saw as many as four in each transverse line. Has this enigmatical canal anything to do with the ‘typhlosole’ of the earthworm ?

On the dorsal surface of the head a longitudinal canal, which sometimes appears to be ciliated, was visible at *b* (fig. 3) ; posteriorly it divided into two branches which dilated into granular cæca, arranged in a kind of festoon in the first segment of the thorax.

The coloration of this part of the body prevented me from determining whether this canal opened externally or into the œsophagus, and also whether it was in any way connected with the ventral ciliated canal,—both of them points of much interest.

[1] This cæcal termination of the vessels appears to reach its greatest development in the Scoleid genera, Euaxes and Lumbriculus, in which a vessel arises in each segment from the dorsal trunk, and shortly divides into many cæcal ramuscules. See Siebold, Vegleichende Anatomie, p. 212.

[2] The general contractility of the vessels of the annelids has already been pointed out by De Quatrefages. Siebold doubts the existence of a regular circulation in the majority of the *Annelida*. *Ob. cit.*, p. 210.

However this may be, these sacs are clearly homologous with the curious sacs which have been described in *Chlorœma*, and perhaps with the sacs opening externally, which are found in the anterior segment of *Pectinaria.*

I may mention here that ciliated organs, possibly homologous with these, and with the lateral convoluted canals of the *Lumbricidæ* and *Hirudinidæ* are by no means uncommon among the *Annelida Errantia*, and may be observed in *Phyllodoce;* it requires care however to discover them.

Nervous system.—On this head the result of my examinations was exceedingly unsatisfactory, as I could assure myself of the existence of only two oval ganglia, one on each side of the œsophagus, each of which presented a dark pigment mass (eyespot ?) on its anterior extremity.

Reproductive elements.—Protula Dysteri can hardly be said to possess special reproductive organs, the reproductive elements, viz., ova and spermatozoa, being developed as it were accidentally from the walls of the perivisceral cavity, by the fluid contained in which (whose nature and importance M. de Quatrefages has so well pointed out) they are bathed, and supplied with nutritive materials. It appeared to me that the spermatozoa or ova took their origin in granular thickenings of that portion of the face of the dissepiments which is traversed by the transverse vessel, becoming detached thence, and floating freely in the perivisceral fluid, as they attained their full development.[1]

The youngest spermatozoa were minute spherules, of not more than $\frac{1}{5000}$ of an inch in diameter, aggregated together into irregular masses (fig. 11). In a more advanced state a very fine short and delicate filament could be observed springing from one side of this body. By degrees the spherule became elliptical, and narrowing *pari passu* with the elongation and thickening of the filament, the ultimate result was a spermatozoon, such as that represented in fig. 11, with a subcylindrical slightly pointed head of $\frac{1}{3500}$ of an inch in diameter, and a very long actively-undulating tail.

The ova are, at first, very small, not more than $\frac{1}{4000}$ of an inch in diameter, and possess a relatively very large, clear space, representing the germinal vesicles, containing a minute germinal spot. By degrees they increase in size to $\frac{1}{600}$ inch, with a germinal vesicle of $\frac{1}{1000}$, and

[1] Frey and Leuckart (Zool. Untersuchungen, p. 88) assert that the generative elements of the annelids are developed from a free blastema, and not from the septa only, as Krohn asserts to be the case in Alciope, and as I should, from what is stated above, be disposed to believe.

a spot of $\frac{1}{3500}$, and a few granules become visible in their yelk. From this size they gradually increase to the $\frac{1}{150}$ inch in diameter, acquiring a well-marked vitellary membrane, and a dark orange-red, very coarsely granular yelk. The germinal vesicle and spot may still be rendered visible by pressure, the former being about $\frac{1}{600}$ of an inch in diameter.

When those segments of the body in which the genitalia are situated were subjected to moderate pressure, the spermatozoa made their exit at the bases of the pedal tubercules of the male segments, while the ova, just giving rise to bulgings in a corresponding position, eventually passed out in the same manner. I could not satisfactorily decide, however, whether the apertures by which the generative products passed out were natural or artificial.[1]

Setæ and Uncini of the Pedal Tubercles.—The general form of the pedal tubercles has already been described; it remains only, therefore, to note more particularly the form of their appendages, whether *Setæ or Uncini.* The *Setæ* (figs. 7, 8) are slender spines, about $\frac{1}{80}$ of an inch in length, consisting of a haft and a blade; the former is about six times the length of the latter, and is rounded, flattened gradually as it passes into the blade, with which it is completely continuous, though at an obtuse angle.[2] The blade tapers gradually to its point, and is smooth on one edge, but minutely denticulated upon the other, while delicate striæ are continued from the serrations upon the flat face of the blade.

Such is the structure of those stronger setæ which are directed forwards on each side of the head-lobe. Those of the posterior segments have a similar general structure, but are more delicate.

The *uncini* (figs. 7, 8) are very small, not more than $\frac{1}{1000}$ inch in length; and it is not easy to make out their exact structure. Each, however, appears to be composed of a short implanted stem, and a blade set upon the end of this, at somewhat less than a right angle, like the claw of a hammer. The edges of this blade are minutely denticulated.

Fissiparous multiplication.—It was only a minority of the *Protulæ* which presented the aspect hitherto described; for the larger number

[1] It should be added that the genital products occupy about fourteen successive segments of the abdomen, of which the two anterior are seminiferous; the rest, ovigerous. See Fig. 3.

[2] I am not aware of any annelid in which the setæ are really articulated. The statements of Audouin and Milne-Edwards rest, I believe, upon errors of observation, very intelligible, if one considers what microscopes were twenty years ago. How such strange perversions of fact as the figures of annelid setæ appended to Dr. Williams's Report on the British Annelida, published in the Transactions of the British Association for 1851—can have arisen, it is not so easy to comprehend.

were undergoing multiplication or prolification, by a process which can only be described as a combined fission and gemmation. The prolification takes place so as to separate all the segments of the parent behind the sixteenth, as a new zooid ; but it is not a mere process of fission, for the seventeenth segment, *i.e.*, the first of the new zooid, undergoes a very considerable enlargement, and eventually becomes divided into the nine segments of the head and thorax, of the bud. These segments do not appear all at once, but gradually, one behind the other. The intestinal canal of the stock and of the bud are at first perfectly continuous, but the peri-intestinal cavity of the bud is completely filled with a mass of red granules. These would seem in some way to subserve the nutrition of the young animal ; for in some free zooids, apparently fully formed, all but the development of genitalia, the caudal segments were full of these orange granules, while no trace of them was to be found anteriorly.[1]

It is very interesting to note the manner in which the branchial plumes are developed, as it closely corresponds with what Milne-Edwards describes in *Terebella*. Each plume appears at first as a quadrate palmate process of the dorsal side of the first segment ; and the divisions representing the stems of the future branchiæ are at first mere processes,—perfectly simple tubes, which do not even present annulations.

Several modes of prolification are already known to exist among the annelids. The one long since described by O. F. Müller, as one of the methods of multiplication of *Nais*, and more lately by Quatrefages as occurring in *Syllis prolifera* is very nearly simple fission, the animal dividing near its middle, and the under half, before separation, only putting forth, as buds, those appendages which are characteristic of the head.

Secondly, Milne-Edwards has described in *Myriadina* a prolification by a sort of continuous budding between the anal and the penultimate segment. A new ring is produced behind the penultimate segment, and this enlarging gives rise to a new ring posteriorly, and so on until the bud attains its full length.

It would seen possible that the second mode of prolification in *Nais*, described by O. F. Müller, is in reality the same as this, though he describes the new growth as entirely resulting from the excessive development of the anal segment.

Thirdly, M. Schulze, an excellent observer, has described a third very singular mode of prolification in *Nais*, whence the long chains of

[1] Sars gives an account of the prolification of Filograna implexa, similar in all essential points. See his Fauna littoralis, &c., pp. 88–9.

zooids occasionally observed arise. For when, by the fissive process the *Nais* is divided into an anterior and posterior zooid, the last segment of the former greatly enlarges, becomes divided into segments, and the anterior of these becoming a head, a new zooid is formed between the previously existing ones ; this process is repeated in what was the penultimate, but is now the ultimate segment of the anterior zooid : and, again, in the anti-penultimate, so that at least a long string of zooids is formed, each of which, except the last, is produced from a single segment.

Fourthly, According to Frey and Leuckart, whose observations have been confirmed by Krohn (Wieg. Archiv., 1852), *Autolytus prolifer* multiplies in a somewhat similar way, but instead of each new interposed zooid being formed at the expense of a fresh segment of the anterior zooid—it is produced by the metamorphosis of a bud, or rather of a mass of blastema the equivalent of a bud, developed from the under extremity of the last segment of the anterior zooid.

Supposing further observation to confirm the distinctness of all these modes of prolification, they might be classified according to the amount of the already formed parental organism which enters into the produced zooid.

1. All the segments of the latter were segments of the former, the new products being merely cephalic organs.

2. None of the segments of the produced zooid belonged to the parent zooid, but the former is a metamorphosis of a whole segment of the latter.

3. None of the segments of the produced zooid belonged to the parent zooid, and the former contains hardly any of the primitive substance of the latter, being developed by germination from its last segment.

It is clear that the prolification of *Protula Dysteri* will come under none of these categories ; but is a combination of the first and second methods. The abdomen of the produced zooid is a mere fissive product of the parent, but its thorax is the result of the metamorphosis of a single segment of the parent into many segments.

Quatrefages endeavoured to show that the relation of the produced zooids of *Syllis* to the anterior zooid was that of an "alternation of generation," the former alone developing sexual products. Krohn has however proved that no such relation exists in this case ; but on the other hand he brings forward good evidence to demonstrate that the posterior zooids of *Autolytus prolifer* really *are* generative zooids, and alone develop the reproductive elements. The male zooids in this case are widely different from the gemmiparous zooid ; so dif-

ferent, in fact, that they were regarded by O. F. Müller as belonging to a distinct species.

I sought carefully for evidence of any such "alternation" in *Protula Dysteri*, but the result was to convince myself that nothing of the kind exists.

The generative products may indeed almost always be detected, though the ova are very small and indistinct, in the anterior zooid of any still unseparated pair; and it is therefore clear that the gemmiparous zooid is not asexual, the invariable rule where that separation of the individual into asexual and sexual zooids, which constitutes the so-called "alternation of generations," really exists.

DESCRIPTION OF FIGURES.

Pl. I. [XXVI.]

Fig. 1. Vermidom of *Protula Dysteri.*

Fig. 2. Single calcareous tube with the worm protruded and expanded.

Fig. 3. An adult *Protula* extracted from its case, *b.* branchia, *c.* testes, *d.* ova, (dorsal view).

Fig. 4. *A Protula* undergoing prolification (central view).

Fig. 5. The produced zooid just set free.

Fig. 6. Junction of parent and derivative zooids (ventral view), *a.* ciliated canal.

Fig. 7. Pedal tubercle.

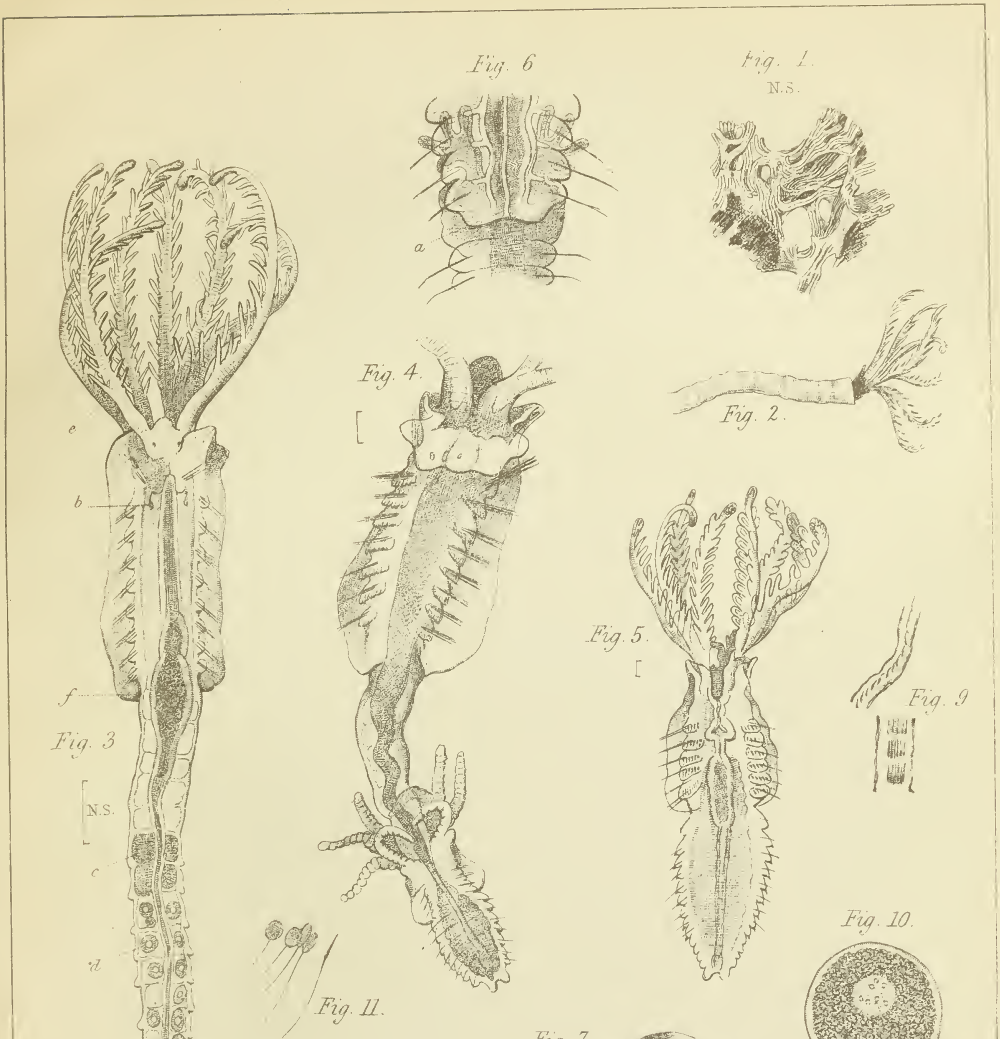
Fig. 8. *Setæ and Uncini.*

Fig. 9. Ciliated canal, greatly magnified.

Fig. 10. Ova—young and completely developed.

Fig. 11. Spermatozoa—young and completely developed.

[PLATE XXVI]



ad nat. del. T.H.H.

J. Basire sc.

XXXIV

ON THE STRUCTURE OF NOCTILUCA MILIARIS

Quart. Journ. Microsc. Sci., vol. iii., 1855, *pp.* 49-54

AMONG the many striking and beautiful appearances presented by the Ocean, there is none, perhaps, which has more attracted the attention both of the naturalist and of the casual observer, than the silvery, sparkling, phosphorescent light, which may often be seen on dark nights, illuminating the track of every boat and defining the contours of the waves as they break upon the shore.

After long serving as a fertile subject of doubt and discussion, it is now well known that this luminosity proceeds from many sources; in the main, from living invertebrate animals—Protozoa, Polypes, Medusæ, Annelids, Crustaceans, &c. Among these again, the chief and most important part is played, as was first shown in the middle of the last century by M. Rigaut, and again in 1810 by M. Suriray,[1] by a singular and anomalous creature of very simple organization, the *Noctiluca miliaris*.

According to M. Suriray the *Noctiluca* is a spherical gelatinous mass, provided with a long filiform tentacle or appendage, presenting a mouth, an œsophagus, one or many stomachs and ramified ovaries, and thus possessing a certain complexity of organization. De Blainville confirmed Suriray's account, and placed *Noctiluca*, without doubt most erroneously, among the Diphydæ. On the other hand, Van Beneden Verhaeghe and Doyére, denying the relation of *Noctiluca* with the Acalephæ—and conceiving its organization to be of a much more elementary character—relegated it to the Rhizopoda.

[1] See *Quatrefages, l. c.* I regret that I have not access at this moment to M. Suriray's paper.

To this doctrine M. de Quatrefages also attaches the weight of his authority in his valuable essay '*Observations sur les Noctiluques*,' published in the Annales des Sciences Nat. for 1850. M. de Quatrefages does not admit the existence of any true mouth or intestinal canal, and considers that the so-called stomachs are nothing but '*vacuoles*' similar to those observed in the Rhizopoda and Infusoria.

In a short memoir published in Wiegmann's Archiv. for 1852, however, that excellent and most accurate observer, M. Krohn, carried the subject a stage further, and showed that the organization of *Noctiluca* is more complex than has been supposed. Krohn carefully describes and figures the mouth of *Noctiluca* and the long vibratile *cilium*, which he was the first to observe, proceeding from it. Krohn draws particular attention to the oval body first described by Verhaeghe, which he considers to be the homologue of the '*nucleus*' of the infusoria; and describes the ejection of fæcal matters. Arranging the *Noctiluca* among the Protozoa, Krohn points out some interesting structural analogies with *Actinophrys* and *Paramœcium*.

I will now proceed to detail the results of my own observations.

Noctiluca miliaris (Plate V. [XXVII.] figs. 1, 2) may be best described as a gelatinous transparent body, about 1–60th[1] of an inch in diameter, and having very nearly the form of a peach; that is to say, one surface is a little excavated and a groove or depression runs from one side of the excavation half way to the other pole (*échancrure*, Quatrefages. *Frauenbnsenähnliche Einbucht*, Krohn). Where the stalk of the peach might be, a filiform tentacle, equal in length to about the diameter of the body, depends from it, and exhibits slow wavy motions when the creature is in full activity. I have even seen a *Noctiluca* appear to push repeatedly against obstacles, with this tentacle.

The body is composed of a structureless and somewhat dense external membrane, which is continued on to the tentacle. Beneath this is a layer of granules or rather a gelatinous membrane, through whose substance minute granules are scattered without any very definite arrangement. From hence arises a network of very delicate fibrils, whose meshes are not more than 1–3000th of an inch in diameter (fig. 6), and these gradually pass internally,—the reticulation becoming more and more open—into coarser fibres, which take a convergent direction towards the stomach and *nucleus*. All these fibres and fibrils are covered with minute granules, which are usually larger towards the centre.

[1] The extremes of size are given by Krohn as 1–7—1 millimetre = 1–170—1–25 inch about.

Quatrefages states that these granules may be seen to glide from the centre to the circumference, and *vice versa*, propelled by the contractions or expansions of the transparent matrix in which they are imbedded ; that new fibrous processes (*expansions*) arise on the central mass and unite, dividing and subdividing, with the neighbouring ones—and that if the creature be irritated, the fibres and fibrils become detached from the investing membrane, and are drawn in towards the mouth "like threads of a very viscid liquid, which retract slowly after being broken."

All these appearances may be very readily seen ; but I am strongly inclined to believe that the greater part of them are abnormal states, and that in their natural and perfectly unaltered condition, the fibres and fibrils are perfectly quiescent, and present nothing to be compared with the protean movements of the *Amœbæ*. In their perfectly fresh and unchanged state, in fact, the fibrous network is by no means so obvious as it usually appears, and in such specimens I have been unable to convince myself that the granules undergo any change of place—certainly there is no protrusion and retraction of processes to be compared with that which takes place in the Rhizopoda.[1]

The oral aperture has been satisfactorily described by Krohn. Supposing the animal to lie upon its oral face (the attitude it commonly assumes), with its tentacle forwards—the oral aperture appears as a sort of half oval, with a nearly straight edge anteriorly, and a deeply-curved outline posteriorly (fig. 4).

The anterior edge is not quite straight, but is formed by two ridges, apparently of a harder substance than the remainder of the outer membrane, which run up on the two sides of the fissure, and unite, forming a very obtuse angle, open anteriorly, in the base of the tentacle.

The latter is a subcylindrical filament of 1–1800th inch diameter, more or less flattened, sometimes quite flat at its free end, which is rounded at the apex. It is a little broader at its base than elsewhere, and consists of an external structureless membrane continuous with the general investment, and of an internal substance, which is so marked by transverse granular lines, as very closely to resemble a primitive fibril of striped muscle. I agree with Krohn that the striation is not in the external membrane, as Quatrefages states.

From the bottom of the oral cavity a very delicate filament (fig. 3), which exhibits a rapid undulating motion, is occasionally protruded

[1] Krohn states, that he could hardly ever cause the *Noctilucæ* to contract by mechanical or chemical irritation ; but that he once saw one which repeatedly contracted before falling into the permanently wrinkled and collapsed condition, into which they so readily pass.

and then suddenly withdrawn. Krohn, who first discovered this singular organ, considers that it plays an important part in sweeping nutritive matters into the oral cavity, and there can be little doubt that such is the case. I would warn future observers not to be easily discouraged in their search for this organ. I had sought for it in at least fifty individuals without success; and nothing but the firm confidence in M. Krohn's accuracy, with which frequent working over his ground has inspired me, led me to persevere until I had discovered it. Among the great numbers of *Noctilucæ* which I examined, however, I did not observe half a dozen which presented a good view of the *cilium*.

Under these circumstances, I do not comprehend how it is that M. Krohn should have overlooked a very remarkable structure which requires no such sharpness of vision as that to which I have just alluded. I refer to an S-shaped ridge arising close to the right extremity of the anterior oral margin above described, and passing down on the right side of the oral aperture to form its lateral and posterior boundary.

This ridge is horny-looking, and is considerably produced in its middle portion into a tricuspid prominence (fig. 4 *d*), for which I know of no better name than a 'tooth.' This tooth is about 1–7000th in. high; its middle cusp is stronger than the other two, and bifid, while the posterior has a slight pointed heel. I have never observed any movement in this tooth-like body.

Behind it the oral aperture narrows to inclose what may be termed a *post-oral* space, and then widens again; the elevations bordering this post-oral space are continuous with those which form the sides of the triangular groove or fissure, which has been above described as running up on one side of the body (figs. 1, 2 *b*). In the midst of this flattened post-oral space there is a small funnel-shaped depression which I am strongly inclined to believe is an anal aperture (fig. 3 *f*).

The oral aperture leads into the granular mass of the alimentary cavity, from which the fibres and fibrils radiate. Quatrefages says:—

"At one part of the groove of which we have spoken, and near the point of insertion of the appendage, there is always a little mass of different substances, sand, &c., which can only be detached with great difficulty. When this has been done these foreign bodies are seen to have simply adhered to a semi-transparent, granular substance, which projects like a hernia, so to say, from a little orifice (mouth of authors) by which the membranes are perforated. This external substance is continuous with a much larger internal mass of the same nature, whose dimensions and form vary in each individual.

"However carefully I have sought for a digestive canal of any kind, I have never been able to discover anything of the sort; but I have very frequently seen more or less considerable vacuoles in the midst of this substance. It is these most probably which have been regarded as stomachs by MM. de Blainville and Suriray."

I have never seen this projecting mass nor any foreign bodies in the position indicated by Quatrefages, in perfectly fresh specimens. In those which had undergone alteration, on the other hand, such an appearance was frequent, but it invariably appeared to me to result from a partial extrusion of the contents of the stomach.

The appearance of 'vacuoles,' on the other hand, is almost invariable in fresh specimens; but I cannot think that these clear spaces, which are defined by a well-marked membranous wall, have any analogy with the shifting 'vacuoles' of the Infusoria and Rhizopods. It appeared to me, on the other hand, that the oral cavity led directly into a definite stomach, whose walls are capable of very great local dilatation, such dilatations, connected by very narrow pedicles with the central cavity, then having all the appearance of independent vacuoles (fig. 3 *e*). The accumulation of granules around the central mass greatly contributes to this appearance. Like Krohn, I frequently noticed large Diatomaceæ and other foreign matters in these gastric pouches.

Not only does all I have observed lead me to believe that *Noctiluca* has a definite alimentary cavity, but I am, as I have said above, inclined to think that this cavity has an excretory aperture distinct from the mouth. The funnel-shaped depression in the post-oral area, in fact, always appeared, when I could obtain a favourable view, to be connected with a special process of the stomach. On one occasion I observed the sides of this process to be surrounded by fusiform transversely-striated fibres or folds, I could not determine which.

Krohn states that he repeatedly saw the *egesta* voided 'in the neighbourhood of the groove of the body,' but he could not determine at what exact point, and he inclines to think it must have taken place through the mouth.

I am equally unable to bring forward direct evidence on this point, and my belief in the existence of a distinct *anus* is founded simply on the structural appearances.

In front of and above the gastric cavity is the *nucleus* (*c*), described by Verhaeghe and Krohn. This is a strongly refracting, oval body of about 1–460th inch in length, which, by the action of acetic acid, assumes the appearance of a hollow vesicle. The anterior radiating fibres pass from it; the posterior from the alimentary canal.

Quatrefages and Krohn consider that a process of fissiparous multiplication takes place in *Noctiluca*; both of these observers having found double individuals, though very rarely. According to the latter writer, division of the body is preceded by that of the *nucleus*. I have not had the good fortune to meet with any of these forms, and the only indication of a possible reproductive apparatus which I have seen consisted of a number of granular, vesicular bodies (fig. 5 *h*), of about 1-2000th inch in diameter, scattered over the surface of the anterior and inferior part of the body.

Such is what repeated examination leads me to believe is the structure of *Noctiluca*; but if the preceding account be correct it is obvious that the animal is no Rhizopod, but must be promoted from the lowest ranks of the Protozoa to the highest.

The existence of a dental armature and of a distinct anal aperture, are structural peculiarities which greatly increase the affinity to such forms as *Colpoda* and *Paramœcium*, indicated by Krohn. *Noctiluca* might be regarded as a gigantic Infusorium with the grooved body of *Colpoda*, the long process of *Trachelius*, and the dental armature of *Nassula* united in one animal.

On the other hand, the general absence of *cilia* over the body, and the wide differences in detail, would require the constitution of at least a distinct family for this singular creature.

DESCRIPTION OF PLATE V. [XXVII.]

Fig. 1. *Noctiluca miliaris*, from above.

Fig. 2. The animal viewed from behind, showing the groove.

Fig. 3. A latero-inferior view, displaying the oral aperture, the cilium, the tooth, a gastric pouch, and the anal (?) aperture.

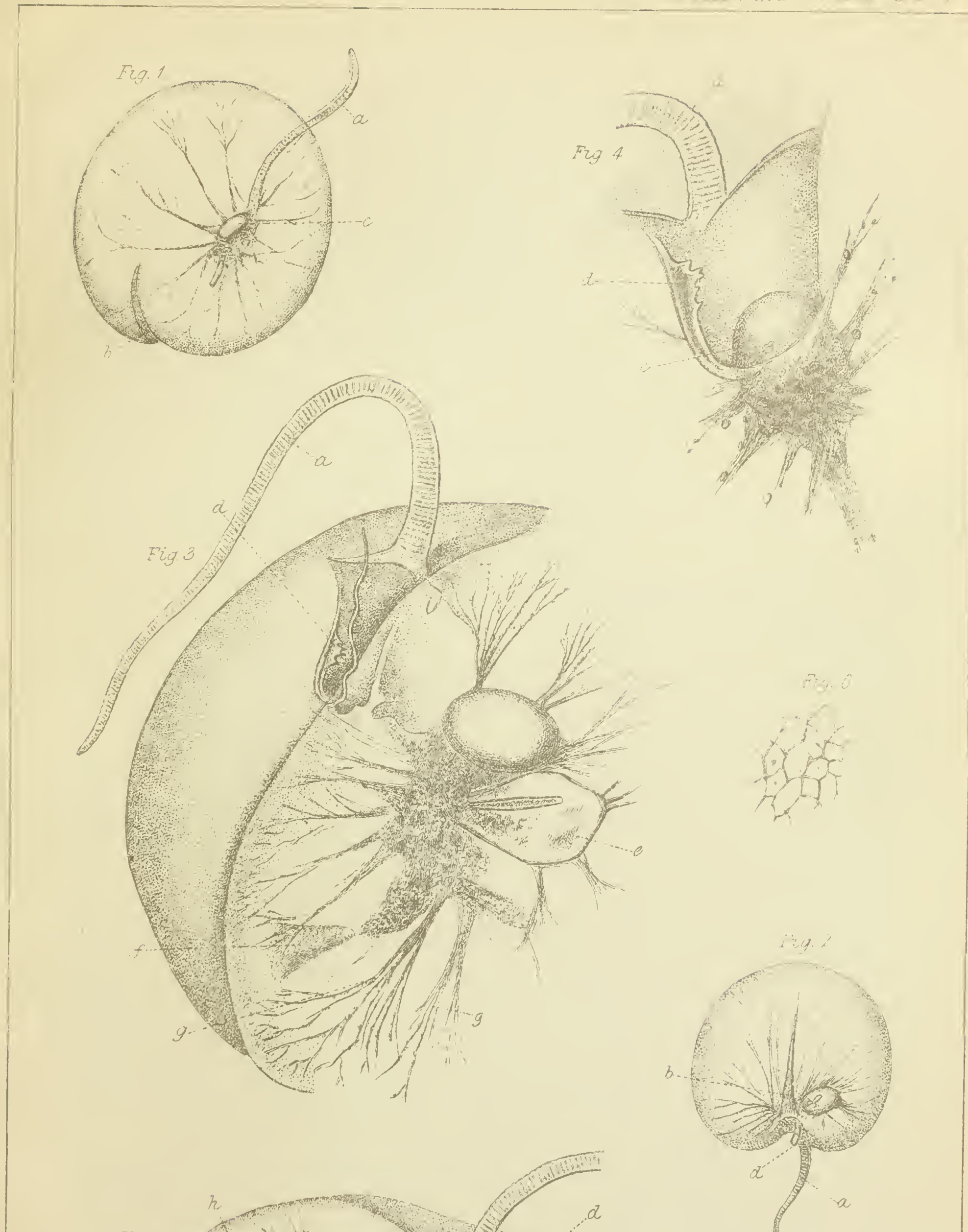
Fig. 4. Theoral aperture on a larger scale.

Fig. 5. Antero-superior view, showing the nucleus, the fibres and fibrils, the tooth and reproductive (?) granules.

Fig. 6. The superficial network of granules and fibrils. *a*. Tentacle. *b*. Groove. *c*. Nucleus. *d*. Tooth. *e*. Gastric pouches. *f*. Anal aperture. *g*. Radiating fibres and fibrils. *h*. Reproductive (?) granules.

[PLATE XXVII]

To face p. 356.



XXXV

ON THE ENAMEL AND DENTINE OF THE TEETH

Quart. Journ. Microsc. Sci., vol. iii., 1855, *pp.* 127–130

THE first part of the sixth volume of Siebold and Kölliker's 'Zeitschrift für Wissenschaftliche Zoologie,' published in July of the present year, contains a paper by M. Edouard Lent, 'On the Development of the Dentine and Enamel of the Teeth.' It could only be a source of gratification to me that any one should have been led fairly to investigate a subject, by the perusal of a paper of mine published in this Journal, even if his results were totally opposed to those at which I had arrived; and I do not think that, as a general rule, controversial writing is worth the paper it is printed on—assuredly, it is not worth the time it wastes. I should, therefore, have had nothing to reply to M. Lent's unfavourable expressions with regard to my labours, were it not for two circumstances. In the first place, M. Lent is a pupil of Professor Kölliker's, and appears to have worked under the eye of that distinguished investigator. Indeed, the paper is so completely sanctioned by Professor Kölliker, that I must regard him as responsible for it. And in the second place, owing, as I suppose, to M. Lent's inexperience as an author (though truly the superintendence of so practised a writer as Professor Kölliker should have obviated this difficulty), his paper is curiously inconsistent with itself, being in form a severe criticism and refutation—but, in fact, a confirmation—of the views I ventured to promulgate.

My paper was intended to establish two main points—1. That there is no evidence that the dentine is formed by direct conversion of pre-existing elements of the pulp. 2. That the enamel is not developed externally to the so-called basement membrane, or mem-

brana preformativa of the pulp, but internally to it; Nasmyth's membrane, which lies over the enamel, being in fact continuous with the membrana preformativa.

1. On this head, M. Lent adds no new fact or argument of any kind. He simply repeats and confirms the statement already made by Professor Kölliker—that minute gelatinous processes may often be found passing from the surface of the pulp into the dentinal canals (a statement which no one denies), and then takes for granted Professor Kölliker's purely hypothetical interpretation of this fact—*i.e.*, that these processes are outgrowths of the "cells" of the surface of the pulp—an hypothesis which is not supported, so far as I am aware, by a shadow of direct evidence; and it is to be remembered that the *fact* is as well accounted for by my hypothesis as by any other.

So much for the formation of the dentinal tubules. With regard to the substance of the dentine, M. Lent does not seem to have seen much more than myself; for he says that "it is more probable—indeed certain" that the "grund-substanz" is an "*excretion of the cells and their processes.*" (P. 127.)

That is to say, M. Lent (*i.e.* Professor Kölliker) admits that there is no new evidence to be brought forward as to the formation of the dentine tubules, and that the substance of the dentine is formed as I have stated it to be. Truly, then, I do not see where the "*irrige ansicht*" with which I am charged lies.

At page 128 there is a very careless misstatement, which one might be disposed to overlook in a student, but which is utterly unpardonable in a production which has the advantage of Professor Kölliker's deliberate *imprimatur*.

"As regards Huxley's erroneous view as to the formation of the dentine, I will only briefly remark, that Huxley has been so unfortunate as to have seen the dentine from above only." (p. 128.)

This is truly astounding, considering that at page 160 of my paper I give particular directions how to obtain a profile view of the dentine in undisturbed connexion with the pulp; that figs. 3 and 4 are careful representations of such profile views; and that I lay particular stress upon the advantages to be derived from this mode of examination.

2. With regard to the development of the enamel, M. Lent (*i.e.* Professor Kölliker) affords a confirmation of my views; all the more valuable, as it is evidently most unwillingly wrung from him.

At page 129, M. Lent, after stating the ordinary theory of the development of the enamel, says: "This simple theory must, however, I believe, be given up, since Huxley has made a discovery whose

truth I must confirm—a discovery which greatly enhances the difficulty of accounting for the formation of the enamel."

Again at page 133: "From what has been said, it is pretty clear that the membrana preformativa, which may be detached from the enamel in the fœtal tooth, subsequently becomes the so-called cuticle of the enamel, as, indeed, Huxley states."

Again, at page 130: "When, however, I tested Huxley's new statements, the matter appeared in quite a new light—the more as I could never succeed in discovering a trace of a nucleus in an enamel prism. Huxley, in fact, asserts that the enamel is formed beneath the membrana preformativa, and that the membrana preformativa and cuticle of the enamel are identical. In this point—as I have found by examining the fresh teeth of a new-born child and those of a six months' fœtus—he is about right"

I wish I could give the entire force of M. Lent's exquisite and polite acknowledgment of the truth of a fundamental fact for all further theories of dental development, but here is the original, for those who can appreciate it: "*Hiermit hat es seine Richtigkeit.*"

In this part of M. Lent's paper a second misstatement occurs, somewhat more gross, if possible, than that which I have already had occasion to notice.

At page 131 he says: "Of nuclei such as Huxley describes and figures (in the membrana preformativa), I have seen nothing."

I have carefully re-examined my own paper, to see if I could find any excuse for a statement so utterly contrary to fact as this; and, for the sake of MM. Lent and Kölliker, I really almost regret to say I can find none whatever.

I invariably call the membrana preformativa a *structureless membrane.* I state that Nasmyth's membrane is "about 1–2500th to 1–1600th inch thick, perfectly clear and transparent, and, under a high power, exhibits innumerable little ridges upon its outer surface, which bound spaces sometimes oval and sometimes quadrangular, and about 1–1500th of an inch in diameter." And I go on to say that this membrane is nothing but the altered structureless membrana preformativa. I am equally at a loss to discover any figures of these "nuclei;" though it is possible that in consequence of the reticulation not having been carried evenly all over Nasmyth's membrane in fig. 2, a very careless person might misunderstand the figure—the text however, would at once correct this misapprehension.

I have neither space nor inclination to follow M. Lent further; as what has been said proves abundantly the only point worth discussing at all: viz., that the two main facts asserted in my paper are admitted

to be *bona fide* additions to our knowledge ; in fact, one might almost fancy M. Kölliker addressing to M. Lent, Balak's famous reproach to Balaam—" I called upon thee to curse this people, and, lo ! thou hast blessed them these many times."

So far as I am personally concerned, I care little enough about being absorbed, after Professor Kölliker's ordinary fashion, in the next edition of the 'Mikroskopische Anatomie,' where we shall, I doubt not, read, " I and Huxley have made out that the enamel is formed under the membrana preformativa," &c., &c. But I think that Professor Kölliker will do well to reflect whether he is likely to increase his most deservedly high reputation by encouraging in a student a disingenuousness of which he himself, I hope, would be heartily ashamed.

I may add, in conclusion, that there are, I believe, two very good minor grounds of cavil in my paper. One is at page 159, where I state incidentally that Professor Kölliker does not mention Nasmyth's discovery in his 'Mikroskopische Anatomie'—an error for which I cannot account, and for which I can only apologise, as a complete oversight. The other is the description of the cement of the calf's tooth at page 162 ; in which a subsequent examination has led me to think there are errors of interpretation. I have had no leisure to re-examine this point, and I recommend it to MM. Lent and Kölliker, if, as it would seem, they have some unaccountable source of satisfaction in finding me wrong—a thing I do myself, quite without satisfaction, every day.

XXXVI

MEMOIR ON PHYSALIA

Linn. Soc. Proc., vol. ii., 1855, *pp.* 3–5

THE specimens of *Physalia* on which Mr. Huxley's observations were made, were collected on board the Rattlesnake, between the 25th of February and the 3rd of March, between lat. 25° and 37° S. and long. 5° and 7° W. They varied in size from $\frac{1}{6}$ in. to 2 in. in the long diameter of the float. The author first describes the general appearance of the specimens, of which he doubts whether the largest were adult, and then proceeds to a minute examination of their details, dividing them for this purpose into the float or air-bladder, and the appendages of greater or less length which depend from it when the animal is in its natural position at the surface of the water. The smaller specimens he states to be the best adapted for examination.

The float is described as consisting of an outer coat, an inner coat and an air-sac contained within them, attached only to one spot of their parietes, and there communicating with the exterior by a small constricted aperture, which was always found on the upper surface. The disposition of the appendages is very irregular, but the larger tentacles are generally placed more externally, the smaller and nascent organs more towards the centre. These appendages are of three kinds, and consist of stomachal sacs, tentacles and cyathiform bodies. Of each of these the author gives a detailed description in their more perfect form, as well as in their undeveloped state as nascent organs ; and then proceeds to inquire, first, what is the physiological importance of the organs described, and secondly, what zoological place should be occupied by an animal provided with such organs so disposed.

Each of these questions the author treats at considerable length.

Of the function of the stomachal sacs in receiving the prey there can be little question ; but it may be doubted whether the digested nutritive matter circulates in the ciliated water-carrying canals or is absorbed into totally different channels. In the latter case the purpose of the stomachal villi would plainly seem to be to absorb nutritive matter and convey it through their central canal to the wide interspace existing between the outer and inner membrane ; but the author states that he has never seen in this interspace any corpuscles analogous to those described by Will as blood-corpuscles. He suggests that the villosities noticed by Dr. Milne-Edwards in the stomachal sacs of *Apolemia* are the same organs, and not ovaries as Dr. Milne-Edwards considers them ; and observes that similar organs exist in a *Diphya* (*Eudoxia*), hereafter to be more fully described. The function of the tentacles, both as prehensile and defensive organs, admits of little doubt ; and on this subject the author notices an erroneous view of M. Lesson, who describes them merely as ducts for conveying an (hypothetical) acrid fluid from an (hypothetical) poison-gland. He also controverts M. Lesson's opinion that certain of the colourless tentacles are to be regarded as branchiæ ; being quite convinced that there is no difference between these and the ordinary tentacles except in the absence of colour. As regards the function of the cyathiform bodies, he has no other than analogical evidence to offer. The only organs in the *Acalephæ* with which he conceives them to have any resemblance are the natatorial organs of the *Physophoræ*. But their little adaptation to a similar purpose, and the entire absence even of their rudiments in young *Physaliæ*, discourage this comparison ; while on the other hand they bear a singular resemblance to the female generative organs of a *Diphya*, and this resemblance extends even to the younger stages of both.

Mr. Huxley concludes by referring *Physalia* to the position assigned to it by Eschscholtz among *Physophoræ*, and near *Discolabe* or *Angela*. In fact, he regards *Physalia* as in all its essential elements nothing but a *Physophora*, whose terminal dilatation has increased at the expense of the rest of the stem, and hence carries all its organs at the base of this dilatation.

The paper was illustrated by pencil drawings of the structures described.

XXXVII

ON THE ANATOMY OF DIPHYES, AND ON THE UNITY OF COMPOSITION OF THE DIPHYIDÆ AND PHYSOPHORIDÆ, &c

Linn. Soc. Proc., vol. ii., 1855, *pp.* 67–69

MR. HUXLEY, whose communication was written at sea, commences his memoir by a brief abstract of previous investigations of the family of *Diphyidæ*, chiefly derived from the works of Lesson and Will, in the absence of other books of reference. Of all the authors referred to, he observes, there is not one except Will, who has given any but a very superficial account of the family. So far even as the natatorial organs are concerned, it is but rarely that a description is sufficiently detailed and accurate not to fit two or three species with equal ease, while the minute internal organs have fared still worse. By all, the important fact of the gemmiparous generation of these animals is overlooked; by all, except Will, the demonstration of the generative organs is omitted, and even he mentions with some doubt the male sac only; and lastly there is no attempt made by any of them to trace the various organs through their development, or to establish on the ground of anatomy the natural affinities of the group. To these latter points, Mr. Huxley states, that his attention has been chiefly directed during a voyage of some months through the South Atlantic and Indian Oceans, in the course of which he has examined several genera both of *Diphyidæ* and *Physophoridæ*, with as much care and attention as the inconveniences of ship-board would permit. The results are given under the following sectional divisions, viz.: 1. a description of the different species examined; 2. their anatomy; and 3. a comparison of *Diphyidæ* and *Physophoridæ*. Under the first head Mr. Huxley describes four species of *Diphyes*,

one of *Calpe*, one of *Eudoxia*, one of *Aglaisma* (?), and one of *Rosacea*. He then enters at length into the anatomy of the different parts of the body, under the several heads of the common tube ; the natatorial organs and the duct connecting their cavities with the common tube ; the nuclear piece or bract and its sacculus ; and the polypoids, each consisting of a stomachal sac, a prehensile organ and a generative organ. Although generative sacs were found by the author in all the genera examined by him, it was only in *Eudoxia* and *Aglaisma* (?) that he procured unequivocal evidence, by the presence of ova, of their real nature. No unequivocal male organs were observed, although the so-called "entozoa" of Will were frequently seen swimming about in the cavity of the young generative organs. But they were not more abundant in these situations than in the stomachal sacs, common tube, &c., and their dissimilarity to true spermatozoa is too great for any conclusions to be founded on their presence. The total absence of male sacs, and the rarity of ova in the females, may, Mr. Huxley thinks, be accounted for by the season during which his investigations were carried on, the months of March, April, May, and June being the winter of the Southern Hemisphere. Lastly, the author enters on the comparative anatomy of various species of *Physophoridæ*, by means of which he believes it to be satisfactorily demonstrated that there exists a unity of organization between the two families of *Diphyidæ* and *Physophoridæ* ; and concludes by stating his opinion that *at least* two other families, the Hydriform and Sertularian Polypes, should be arranged with them in one natural group. The structural coincidences in these families he enumerates as follows : 1. body composed of two membranes, out of which the organs are modelled ; 2. thread-cells universally (?) present ; 3. gemmiparous generation ; 4. sexual generation, spermatozoa and ova being formed in vase-like external sacs.

The paper was accompanied with a series of illustrative drawings.

XXXVIII

TEGUMENTARY ORGANS

The Cyclopædia of Anatomy and Physiology, edited by Robert B. Todd, M.D., F.R.S

The fascicules containing this article were published between August, 1855, *and October,* 1856

In endeavouring to deal with so large a subject as the tegumentary organs of animals, within the limits of an article like the present, it appeared advisable not to attempt to enter into minutiæ of detail (which indeed fall more properly within the province of those who treat of the special classes), but so far as possible to regard these organs as a system in the sense of Bichât—as a sort of zoological class—whose members, the tegumentary organs of particular animals, are but special modifications of one general plan. In reflecting how this might best be done, however, I was met at the outset by certain difficulties and perplexities whose solution appears to me to be essential to any philosophical treatment of the subject, and to the consideration of which I, therefore, propose to devote the following *Preliminary Section.*

§ 1. My first difficulty was to find an answer to the question,—What constitutes a tegumentary organ as distinguished from any other?

The most obvious definition of an *integument* or *tegumentary organ* is, of course,—that which forms the external covering of any animal—*viscus*, on the other hand, being that which is contained. More strictly, it may be said that the integument constitutes that free surface of an animal which is external to the edges of the oral and anal apertures, or where the former alone exists, to *its* edge. Now these definitions are perfectly sufficient so far as surface is concerned; but suppose we make a section perpendicular to the surface, where does integument cease, and where does viscus begin? So far as I am

aware, no elucidation of this point has hitherto been undertaken, and yet, for want of it, the greatest confusion prevails in the nomenclature of those organs which constitute the outer wall of the animal frame.

Intimately connected with this question, and indeed forming a part of it, is a second. In man and the higher animals, there is an universally recognised distinction of the integument into two portions,—the *epidermis* and the *derma ;* and these terms have been extended to all animals. But, if we inquire what constitutes an epidermis, and what a derma, no definite answer is to be met with. It may be said that the derma is vascular, while the epidermis is nonvascular ; or that the epidermis is a simple cellular horny structure, while the derma is complex and fibrous ; but these characters, applicable enough among the higher animals, fail completely with the lower.

Thus, in the majority of the Invertebrata, the derma cannot be said to be vascular, while, on the other hand, the epidermis, or its representative, assumes the structure of fibrous tissue, bone, cartilage, dentine, and enamel,—acquires, in fact, the utmost complexity, and, instead of possessing a horny nature, contains chitin, cellulose or calcareous salts.

Following Mr. Bowman,—who, of course, when he wrote his well-known article on " Mucous Membrane," in this Cyclopædia, could not contemplate the new questions to which the progress of ten years would give rise,—many regard that which is external to a " basement membrane" as epidermic, that which is internal to it, as dermic structure. This test, however, fails us where we most want it ; for among the lower animals, and in some integumentary organs among the higher, membranes identical in structure, or rather in structurelessness, with " basement " membranes, may be met with, forming the surface of what are assuredly epidermic organs.

I believe that here, as elsewhere, the only ultimate appeal lies to development, both as it occurs in the embryo and as it goes on in the adult. What, in fact, is the first process which takes place in the embryo, when the germinal disc is once formed? It is a separation into two layers, by the setting up within the outer portion of the primitive germ of a process of growth independent of that in the inner portion. Where these two areæ or planes of growth, as they might be called, meet, the germ readily separates into two portions, the outer of which is the so-called *serous layer*, the primordial tegumentary system ; while the inner is the *mucous layer*, the primordial viscus. Of course each of these, while *actually* integument and intestine, represents *potentially* a great deal more,—the former, for instance, in the higher animals becoming eventually differentiated into

the proper tegumentary system and a great part of the nervous, the muscular, and the vascular systems; but what I wish to direct attention to at this moment, is the fact, that the first differentiation into integument and viscus proceeds from the setting up of two independent lines, or rather planes of growth, in the germinal membranes.

In the Hydra and Hydroid Polypes generally, we have the essence of this embryonic state as a persistent condition. If, in fact, the body or almost any organ of one of these animals be examined, it will be found (*see* Memoir on the Structure of the Medusæ, Phil. Trans. 1849) to be composed of two distinct membranes, an inner and an outer (*fig.* 303. A). The junction between the two is distinctly marked by a clear line, which would elsewhere be called a basement membrane (*a*). External and internal to this, there is a layer of young tissue, consisting of a homogeneous periplast with minute imbedded endoplasts ("nuclei"). As we proceed towards the free surface, we find that a process of vacuolation and cellulation takes place in the periplast, until the coarsely cellular appearance with which every one is acquainted is produced.

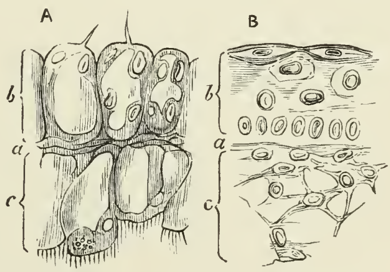


FIG. 303.—A, hydra; *b*, outer membrane; *c*, inner membrane. B, young mammal; *b*, epidermis; *c*, derma.

In the Hydra, then, we have the whole thickness of the body divided into two portions by a line, on each side of which, inwards and outwards, there is an increasing histological metamorphosis or differentiation. There is a median *plane of no differentiation*, as it might be termed, external and internal to which, is a zone of *indifferent tissue*, while, still more remote again, is a zone of *metamorphosed tissue*. The absolute structure of the two layers thus produced is very similar,[1] so much so, that, as is well known, either may perform for a time the function of the other. The distinction between the integument and the mucous membrane in a morphological point of view, however, is as strongly marked as in the most complex animal. The integument, in fact, grows from within outwards—it is endogenous, its youngest portions being internal: the mucous membrane, on the other hand, grows from without inwards—its youngest portion is external, and it is, therefore, exogenous.

We have here, I believe, the fundamental, and the only essential distinction, between true *integumentary* or "*epidermic*" structures and

[1] Though not, as it is commonly said, identical.

all others. *An integumentary or epidermic organ forms or has formed a part of the external surface, and grows endogenously; its youngest portion and plane of no differentiation being directed inwards.*

If, for instance, we compare the young skin of a mammal with the body of the Hydra, we shall find precisely the same planes and zones.

Fig. 303. B, represents a perpendicular section of the integuments of a fœtal lamb 3¼ inches long. (A) marks the position of the line of no differentiation separating the epidermis from the derma; on the outer side of that line lie the close-set endoplasts of the deepest layer (*rete*) of the epidermis, which are disposed somewhat perpendicularly to the surface. On the inner side are the less approximated endoplasts of the outer youngest layer of the derma, more or less parallel to the surface. From *a* to *b*, lies the epidermic area of metamorphosis, the indifferent tissue becoming gradually converted into flattened horny cells. From *a* to *c*, on the other hand, is the dermic area of metamorphosis, the indifferent tissue gradually changing into connective tissue.

It will be observed here, that as the whole serous layer of the germ corresponds in structure with the epidermis only, of the fully formed animal, so the whole integument of the Hydra corresponds with what is usually considered as only a portion of the integument—the *epidermis*—of the mammal. The derma, or true skin of the latter, would not come at all under our present definition of integument, since it has all the morphological characters of the mucous layer of the Hydra, or of the germ; *i.e.* its youngest layer is external, its growth is exogenous, and the metamorphosis of its tissue takes place from within outwards.

In fact, in all animals higher than the Hydroid Polypes (possessing therefore a visceral cavity) we find a complication of structure, corresponding with that which is produced in the germ, when the "*membrana intermedia*" divides into its parietal and intestinal laminæ. Compared with the Hydroid Polypes, the higher forms are double animals, and a section of their bodies is, morphologically speaking, like a section of two Hydræ, one contained within the other. Both the intestinal parietes, and those of the body, present the same distinction into a central *plane of no differentiation*, from which growth and metamorphosis proceed inward and outward on the two respective surfaces, as that observed in the parietes of the Hydra.

The formation of this so-called membrana intermedia, in fact, appears to result from a repetition of the process with gave rise to the two primary layers of the germ. The previously central *plane of no dflierentiation* is replaced by two others, from which growth and

metamorphosis proceed in the same way. The result is, of course, the division of the germ into three layers—a central and two superficial (inner and outer) planes of metamorphosed tissue—and two planes whence growth and metamorphosis proceed.

It results from all this, that, among the higher animals, the true homologue of the integument of the Hydra is the epidermic layer alone. But it would be exceedingly inconvenient to change the accepted meaning of "Integument" on this ground; and, therefore, I shall, throughout the present article, consider as integument—*the outermost plane of indifferent tissue in the animal body, with its external and internal areæ of metamorphosis collectively; these being simply the expressions of two processes of growth in opposite directions, and their line of contact.*

It must not be supposed that this phraseology involves any hypothetical views: the fact that any integumentary organ consists of these three portions will be found to be either distinctly stated or implied by all writers, and is indeed obvious enough on inspection. But though the facts be old enough, this expression of them is unfortunately so new, that I know of no existing terminology by which it can be properly enunciated. The term "Epidermis," for instance, at present, though it denotes the important character of the direction of growth to which I refer, implies even more strongly the simple cellular structure of an organ; so that to speak of "Epidermic" bony or fibrous tissue would sound almost contradictory. Again, all these distinctions, which have been shown to exist between the two elements of the integument, equally hold good with regard to the mucous membranes. Now we have a term "Epithelium" for the epidermic element of the latter; but there is, as far as I know, none for the element which corresponds with the derma. Nor have we any word for the boundary line between the endogenous and exogenous areæ of growth—the term "basement membrane" expressing only an accidental character of the tissue immediately on one or the other sides of that line.

Although with great reluctance, then, I feel compelled to propose two or three new terms, which may have general application, not only to the integumentary organs, but to all other membranes which possess free surfaces and definite directions of growth and metamorphosis.

The boundary line—passing through indifferent tissue—between any two such opposite areæ of growth and metamorphosis, I term the *Protomorphic line.* The whole external (free) area of metamorphosis I call the *Ecderon;* the entire internal (deep) area of metamorphosis, the *Enderon.*

It will be observed that these definitions rest wholly upon the *mode of growth*, and leave altogether out of consideration the *structure* of the resulting tissue. In fact, as I have already said, an extensive study of the integumentary organs convinces one at once that mere structure affords no base for homology; the ecderon, for instance, presenting every variety from the structurelessness of a homogeneous membrane, as in the Tæniadæ, to the complex combination of the so-called enamel, dentine and bone, in the scales of Placoid Fishes.

It is, I venture to think, no small evidence in favour of the importance of these considerations that they enable us to carry still further the doctrine of the identity of structure of plants and animals sketched by Caspar Wolff, and developed in our own times by Schwann. If we make a transverse section of the growing limb of a vertebrate animal, leaving out of consideration, for the moment, the vessels, nerves, and muscles, we observe from the surface inwards, 1st, the ecderonic area of metamorphosis; 2nd, the integumentary protomorphic line; 3rd, the enderonic area of metamorphosis; 4th, the periosteal area of metamorphosis; 5th, the protomorphic line, formed by the indifferent tissue between periosteum and bone; 6th, the osteal area of metamorphosis, within which lies, 7th, the cartilage resulting from the metamorphosis of the tissue of the primitive axis of the limb.

Now, if we compare this with the growing shoot of a young exogenous plant, we meet with exactly the same series from without inwards. There is, 1st, the epidermis, which commonly becomes replaced by a cork or peridermal layer, just as the primary epidermis over a nail is thrust aside by the subjacent and subsequently-formed horny matter; or, as the horny "epidermis" of a Skate is pushed aside and replaced by the calcareous placoid spine. Beneath this lies, 2nd, a protomorphic (or *cambial*) line, from which metamorphosis into periderma goes on outwards, while inwards it passes into, 3rd, the metamorphosed tissue of the mesophlœum. Next to this comes, 4th, the metamorphic area of the endophlœum or liber; within which is, 5th, the protomorphic line of the cambium, which becomes metamorphosed on its inner surface into, 6th, the wood; within which lies, 7th, the pith, the result of the metamorphosis of the primitive axis of the shoot.

I have endeavoured to render these relations obvious by the diagram (*fig.* 304.), which may be taken for a section from centre to surface of a fœtal limb, or of an exogenous branch. *a*, outer protomorphic line between epidermis or periderma and mesophlœum in the plant; between ecderon and enderon in the animal; *a'*, inner protomorphic

line between liber and wood of plant, between bone and periosteum of animal; *b*, *b'*, cork and epidermic layers of plant; cellular epidermis and scale of animal, fish, *e.g.*: *c*, mesophlœum, enderon (derma); *d*, liber, periosteum; *e*, *e'*, wood and pith, bone and cartilage; *x*, axis; *y*, surface.

The consideration of vegetable structures will aid us even further in understanding the manner in which the different varieties of integumentary organs, with which we shall meet, are formed. For it is well known that the outer covering of a plant may ultimately be constituted in one of three ways. 1. The original cellular ecderon may persist unchanged. 2. The "epiderm" persisting, a laminated, but otherwise structureless "*cuticula*," may be developed upon its outer surface, attaining sometimes a very considerable thickness. 3. The original epidermis is cast off, its place being taken by the development of a new layer of different, usually suberous constitution beneath it, which then goes on growing endogenously, and constitutes the permanent integumentary surface. Now, we find a precise parallel for all these conditions in animals. In the soft integument of most Mollusca and Vertebrata the first condition obtains, the general surface of the integument being constituted by the cellular "epidermis."

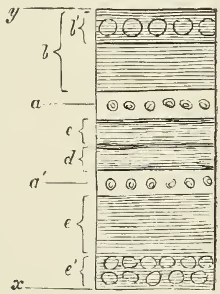


FIG. 304.

In the Annulosa, on the other hand, the integument has certainly, in many cases, and I think probably in the great majority, the character of a vegetable cuticle, consisting as it does of layers developed from the outer surface of the cellular ecderon. In this way also I believe that all molluscan shells are formed.

Lastly, the fish-scale produced altogether beneath the cellular ecderon or epidermis, but growing endogenously after the manner of a true ecderonic structure, appears to be precisely analogous to the corky periderma of the plant; and as the latter, though it is not the original epidermis, takes its place and grows in the same way, so in the fish the scale, which is assuredly not a calcification of the cellular ecderon, yet represents it both in position and in mode of growth.

§ 2 *Morphology of the integuments.*—In the embryonic state of all animals, and in the adult condition of many of the lower forms, the integument, constituted as above defined, forms a continuous investment over the surface of the body without any important processes or

irregularities. Such is the case in many of the Worms, Polypes, and lower Mollusca. From such simple forms of integument as these the most rudimentary kinds of appendages or tegumentary organs are produced in one of two ways,—either the outer portion of the ecderon is thickened, and as a spine or as a plate projects beyond the common surface—*e. g.* cells of Hydroid and Polyzoic Polypes; or the whole integument is developed into a spine-like or plate-shaped process, as in the so-called "bracts" of the Diphydæ, and in all the spines, hairs and scales of the Insecta, Crustacea, and Arachnida.

The shells and plates of Mollusca and Articulata belong principally to the former division, being simply laminated thickenings of the outer portion of the ecderon. In the vertebrata the integument but rarely possesses appendages of so simple a nature. Simple plates of this kind, however, coat the surface of the beaver's tail, in which animal, according to Heusinger, "the epidermis is divided by a great number of clefts into hexagonal portions 4 lines long, whose whole edges adhere to the cutis. They usually consist of a couple of superimposed laminæ identical in structure with the rest of the epidermis" (*l. c.* p. 168.). The polygonal horny plates of the Chelonia are of the same nature. The scales on the under surface of the tail of the rat and other rodents, and on the tarsi of birds, are similarly constituted; but here one edge is thrown up, and we have a transition to the scales of the Pangolin,—to those of Ophidia and Sauria,—and to the nails, claws, hoofs, and hollow horns of Mammals, and the horny sheaths of the beak of Birds, all of which are constructed on essentially the same plan, being diverticula of the whole integument, the outer layer of whose ecderon has undergone horny metamorphosis.

Among these the nails, horns, and hoofs of mammalia present certain complexities of arrangement which entitle them to particular notice.

Nails are flattened horny plates developed from the upper surface of the phalangeal integument only; they are free at their distal extremities, but laterally and at their proximal ends they are enclosed within raised ridges of the whole integuments, the *nail walls.* The enderon beneath them in the space which is called the "bed of the nail" is raised into parallel longitudinal ridges or laminæ, which fit into corresponding depressions of the under surface of the ecderon.

Claws are nails which embrace a larger portion of the phalanx, being developed, not merely from its upper surface, but also from its extremity, and extending far round on its sides. In the dog and cat (*fig.* 305. A) the bed of the claw is laminated as in man, but presents no

papillæ (Gurlt), and a bony plate extends from the last phalanx into the posterior fold of the nail.

The transition from the claw to the *hoof* is readily understood if we suppose the terminal portion of the former to be blunt and cylindrical, instead of pointed and conical (*fig.* 305.). The elephant and rhinoceros do in fact afford an actual passage from the nail to the hoof, inasmuch as their very flat nails are continuous at their edges with the solid and horny covering of the sole (Heusinger).

The solipede hoof has been described in the article SOLIPEDIA; we need therefore only remark here that the *wall* corresponds with the nail in man, and may, by maceration, be separated from the sole and frog, which are developed from the termination and posterior surface of the phalanx. The ridge or "bourrelet" at the upper margin of the wall answers to the posterior nail-wall, and, as in the nail, the horny upper layer of the "epidermis" is continued on to the hoof from it. The structure of the bed of the hoof differs in its different parts. That portion which corresponds with the sole and frog merely presents papillæ, which fit into depressions of the horny ecderon; that which corresponds with the wall is produced into lamellæ like those of the bed of the nail, so that the deep surface of the wall is laminated. In addition, however, long papillæ extend from the "bourrelet" through the superficial portion of the wall, so that, on section, it presents a superficial series of canals, around which the horny matter is disposed in concentric layers.

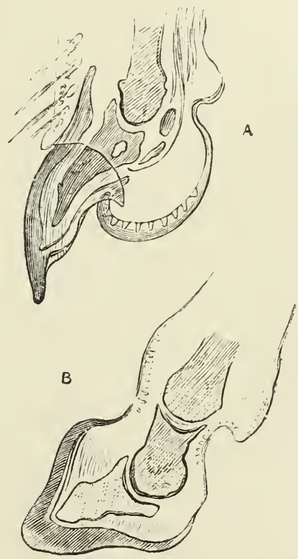


Fig. 305.—A. Section of the foot in the kitten. B. In a fœtal lamb.

Each half of the hoof of a ruminant (*fig.* 305. B), or of the pig, corresponds in general structure with the entire hoof of a solipede, except that the frog is rudimentary. The horny ecderon presents both tubuli and laminæ.

The excrescences on the inner surface of the leg of the horse are identical with the sole of the foot in structure—consisting of a horny mass penetrated by long papillæ.

The hollow *horns* of the Ruminantia are, to all intents and purposes, *Claws*. The superficial cellular ecderon (epidermis) is continued upon them, and, when this is removed, we come to a

laminated fibrous horny mass, which is formed and increased by apposition from the subjacent process of the enderon, supported by its bony axis—a process of the frontal bone. The enderon has neither villi nor lamellæ, presenting only small irregular ridges (Gurlt).

The *horn* of the rhinoceros is commonly said to be constituted by a mass of hairs which have coalesced. However, it consists of an aggregation of tubes, round which the horny matter is arranged in concentric laminæ, as in the horny excrescence of the horse's leg ; and as there is no evidence of its having ever been enclosed within a sac, it is more probable that it belongs to the series of the claws and nails.

Glands, hairs, and feathers.—The *Hairs* and *Spines* of mammals, the *Feathers* of birds, and the *Integumentary Glands* agree in one essential point, that their development is preceded by that of an involution of the ecderon, within which they are formed, and by which the former are, at first, entirely enclosed.

At an early period, the rudiments of the hairs, and those of the cutaneous glands of a fœtal mammal, are indistinguishable. They alike consist of solid processes of the ecderon, consisting of a homogeneous matrix, in which lie closely-set endoplasts, bounded internally by a clear, narrow, transparent "basement membrane," which at once separates them from, and connects them with, the enderon.[1] Externally these processes are continuous with the rete mucosum of the ecderon. In the fœtal lamb, in which I have carefully traced the development of these processes, they increase in size without change of structure, until, in the ordinary hairs, they have attained a length of $\frac{1}{150}$ inch ; for the vibrissæ, that of $\frac{1}{60}$ inch. Having reached this length, it is seen that an accumulation of the indifferent tissue of the enderon has taken place around their cœcal ends, which gradually become pushed in, so that, from being rounded, they appear truncated in section, and present a bulb with a hemispherical involution, the rudiment of the papillæ. In the ordinary hair no special accumulation of indifferent tissue takes place around the body of the involution ; but in the vibrissæ, which are ultimately to possess a thick outer capsule, its foundation appears in this form, and a capillary loop may be seen penetrating the rudimentary papilla.

In the furthest advanced vibrissæ the tissue of the axis of the sac was converted into horny cells, the rudiment of the "fenestrated" or of the inner, horny rootsheath. Over the papilla the rudiment of the hair shaft was indicated by a conical process, horny at its apex and marked by radiating lines. Finally, on each side of the neck of the

[1] The further development of the *glands* will be most conveniently considered, together with their histological structure, below.

sac there was a bulging process, the centre of which was occupied by a mass of fatty-looking granules, the future sebaceous glands of the hair.

Hairs are not normally susceptible of indefinite growth, but have, like the teeth, a fixed form to attain. This form is always that of a more or less elongated spindle, inasmuch as the hairs are sharp at their points, becoming broader and thicker in the middle, and diminishing again at their proximal ends. When fully formed, and ready to fall out, in fact, this end of the hair is either pointed, or more or less ragged and brush-like.

As soon as the finishing process of any hair begins the foundation of a new one is laid by the development of a diverticulum of the outer rootsheath towards its base, in which a young hair is developed, in the manner already described, and gradually pushes out the old one.

The varieties of form and appearance presented by the hairs of animals (for which see the works of Heusinger, Eble, Busk, and Quekett, cited at the end of this article) are produced ; 1st, by the relative proportions of the medullary and cortical substances, and the arrangement of the former with respect to the latter. Thus the peculiar appearance of Rodent hairs is due to the disposition of the medullary substance. 2nd, by the development of the cuticular layer, whence arise the whorled scales of bat's hair—the imbricated plates of seal's hair, &c. ; 3rd, by the shape of the shaft, which may be cylindrical, as in ordinary hair of the head in man ; or evenly flattened, as in the short curly hairs ; or narrow and cylindrical below, and wide and flattened above, as in the hairs of the deer tribe. The spines of certain mammals, such as *Hystrix* and *Erinaceus*, present some interesting peculiarities of form ; offering, as they do, a sort of transition between hairs and feathers.[1]

The porcupine's "quill," as it is called, is a cylindrical tube which gradually diminishes to a point above and below. At its apex the cavity of the quill is simply conical, but lower down its section becomes polygonal, and, the angles of the polygon, being prolonged, resembles a four-rayed star. Still further towards the root of the quill, each ray of the star divides into two secondary rays, and then the secondary rays subdivide into two tertiary rays ; so that eventually the cavity of the spine is a complicated star with four and twenty branches. Below its middle, the quill diminishes in diameter, and at the same time the complexity of its internal cavity likewise disappears, the tertiary rays disappearing first, and then the secondary

[1] See Bröcker (Reichert's Bericht, 1849), from whom the account in the text is taken, though the main points have been independently verified.

&c., until at last the cavity is circular as at the apex. The boundary of the quill cavity is immediately formed by medullary substance; but the cortical substance follows to a certain extent the contour of the inner cavity, so that in a transverse section of the middle of the quill the cortical substance presents the same general outline as the medullary, though its processes and insections are less marked.

In the adult condition, the central cavity is filled by an irregular horny mass, which Reichert and Bröcker regard as the dried-up pulp, but which is probably, as in the feather (*vide infra*), simply the last horny product of the pulp, filling up the space which the latter once occupied; for it is certain that every portion of the porcupine quill has, like every portion of a feather, at one time constituted a cap over the corresponding portion of its pulp. The pulp, in fact, commences like that of a feather, as a smooth conical process upon which the apex of the quill is moulded. As it grows, however, the pulp assumes an angular form, and then, as that of a feather would do, becomes produced into lamellæ. By the constant production of new elements at the surface of these lamellæ and their cornification, the "quill" is produced, and retains internally the impression of the mould on which it was formed. Apart from the arrangement of the lamellæ, the principal difference from a feather which the "quill" presents, is simply that it does not, as it is formed, split up along the lines of the lamellæ of the pulp.

In its main features, the process of development of *feathers* is identical with that of hairs. A solid diverticulum of the ecderon is first formed, within which the primary change consists in the metamorphosis of certain median cells into a cone composed of horny plates. There is thus formed, as in the hair, an outer rootsheath, resembling and continuous with the *rete mucosum*, an inner rootsheath, and a central papilla, the so-called matrix of the feather (*fig.* 306.).

The horny rootsheath (*fig.* 306. *c*) attains a very considerable thickness, and instead of stopping short of the mouth of the sac, as in the hair, its outer end is for a considerable time pushed forwards by its basal growth *pari passu* with that of the feather; so that it eventually projects for a considerable distance beyond the surface. Finally, it opens and allows of the passage of the feather, which grows through it, the horny layer ultimately forming a true rootsheath around the quill. Like the rootsheath of the hair, this structure consists of two layers, an outer (*c*), denser and harder, and an inner (*d*), softer and more flexible. The latter from being marked by the projecting barbs of the young feather has been called the *striated*

sheath. Both layers, however, have the same essential structure, being composed of rounded or polygonal horny plates, whose endoplasts are often distinctly retained even in the outer layers. The histological metamorphosis of the feather will be described below, but the manner in which it acquires its ultimate complex general figure requires particular attention. Every feather consists of the following parts:—*the quill* continuous with the *shaft*, or central axis of the feather, which supports the horizontally expanded *vane*, consisting of numerous long, narrow, flattened laminæ; the *barbs* or primary rays, pointed at their extremities and arranged with their edges upwards and downwards more or less perpendicularly on the shaft. Arranged in a similar manner on the barbs, are the *barbules*, which therefore are disposed more or less parallel to the shaft; from the sides of these lastly, project short, toothed, curved, interlocking *processes*.

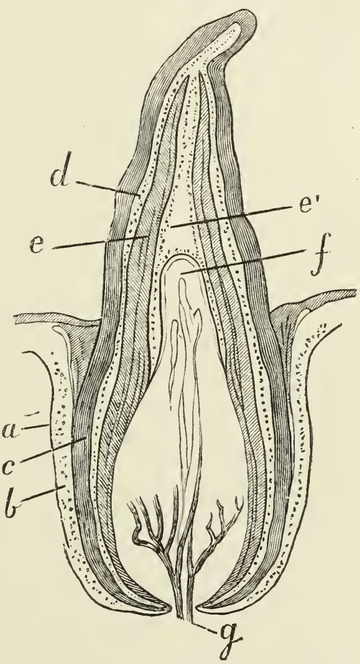


FIG. 306.—Sectional view of feather in its sac: Fowl. *e*, barb; *f*, pulp; *g*, vessel.

All parts of the feather are solid, except the quill, which is hollow and occupied only by a dry shrivelled mass, the *pith*, in its upper part, while below, during life, it receives the pulp. Superiorly, on the under side, where the quill joins the shaft, there is a small aperture, which communicates with the interior, with a short canal in the shaft, and with a groove which runs along its under surface.

It may be well to remember that the apex of a barbule resembles in structure one of its own processes; that of a barb, one of its barbules; that of the shaft, one of its barbs.

The development of this complicated organ from its *matrix* or *pulp* takes place very simply, by a sort of exaggeration of the combination of hair development with that of the nails, which has already been described as occurring in the spines of the porcupine.

On the surface of the feather pulp a series of ridges are developed, running pretty nearly parallel with one another from an antero-posterior groove upon the upper surface, which marks the position of the future shaft, to a line parallel with that groove upon the under surface or

the process, which is called the *raphe.* These ridges, therefore, bound as many grooves which branch off from the medio-dorsal groove, becoming gradually shallower to the raphe. These secondary grooves, as they might be termed however, are not themselves simple; their walls, the ridges, being again produced into short parallel laminæ, and therefore giving rise to tertiary grooves, branching off from the secondary ones. Now, the whole surface of the matrix being covered by an ecderonic layer in process of conversion into the cortical and medullary substances of the feather, the primary groove becomes filled by the end of the shaft; the secondary grooves by the terminal barbs, the tertiary grooves by their barbules, while the processes appear to be outgrowths from these. Were all this conical horny cap to remain entire, the result would be a very complex sort of porcupine's quill; instead of this, however, it breaks up along the line of each ridge, and so we have a feather.

The extremity of the feather being thus constituted, how is its remaining length developed? According to Reichert, the whole pulp elongates, and as fast as a portion of the feather is completed, the corresponding segment of the pulp dries up, constituting for the vane what has been called the *inner striated membrane* (e'). However, I believe that this is not the case, the inner striated membrane being, like the outer, a mass of cornified cells detached from the surface of the pulp, just as we shall see the pith of the shaft to be, though this has been also declared by Reichert to be dried-up pulp. I believe that the growth of the feather, on the other hand, resembles that of the hairs and nails; viz. the extremity as it is finished, is pushed up by the growth of the base, the pulp only supplying materials from its surface; and I account for the inner striated membrane by supposing that a comparatively imperfect development of horny cell membranes takes place from that surface of the pulp which would otherwise be left bare, when the terminal cone or plume of the feather is pushed away. When the development of the shaft has gone on in this manner for a longer or shorter time, according to the length of the feather, a change takes place. The primary groove, which has gradually widened with the width of the shaft (to the exclusion of the secondary grooves, which gradually shorten and ultimately disappear) becoming shallower, extends all round the pulp, and the formation of medullary feather substance ceases, that of cortical substance alone remaining. Thus is the hollow quill formed, and its edges, not quite closing above, leave the minute umbilical aperture by which the inner striated membrane is continued into the "pith" of the quill. This pith is produced by the throwing off of successive transverse horny

partitions from the apex of the pulp, as the quill is pushed beyond it; thus protecting itself from the air admitted by the umbilical aperture, and which is visible, occupying the chambers thus formed (*fig.* 316. G).

There can be no question as to the relations of the integumentary organs hitherto described to the primary constituents of the integuments, but it is different with regard to those calcified tegumentary appendages, the *scales* of Fishes, and the so-called "*dermal*" *calcified plates* of Reptilia and Mammalia. One point is quite certain with regard to these appendages, that they are not, like the calcified shells of the mollusca, the representatives of the outer portion of the originally cellular epidermis (are not therefore comparable to the "cuticula" of a plant), inasmuch as the latter may always, in their young state, be traced over them. It is for this reason, I imagine, that they are at present ordinarily called "dermal" organs. A truly dermal or enderonic organ, however, ought, if it continues to grow, to retain the same characters as the enderon of which it forms a part. It ought, therefore, to have its protomorphic surface external and to grow exogenously. Now, no scale or plate of any fish, so far as I am aware, does this; on the other hand, it holds good of all, whether Placoid, Ganoid, Cycloid or Ctenoid,[1] that they commence by the occurrence of a calcific deposit immediately beneath the cellular ecderon, and that they increase by continual addition to the inner surface of this primary deposit. There are two ways in which we may conceive that these scales and plates are produced. Either they are a gradual calcification of the whole enderon from without inwards (which is the view taken by Leydig, of the scales of Polypterus), in which case the only tissue of the enderon capable of increase (that of the protomorphic line) being arrested by the calcareous deposit, the whole enderon at these parts must cease to grow, which would appear to be contrary to fact; or the scale corresponds with the cork-layer of the vegetable integument, and like it, though developed beneath the ordinary cellular epidermis, is still a truly ecderonic structure.

A great deal might be said for both these views; and if in this place, I assume the latter to be more correct, it is because I think we must be guided by the homology of the scales with certain other organs, where these relations are more definitely expressed. It may be taken as certain, I think, that the scales, plates, and spines of all

[1] And I believe it will be found to be equally true of the "dermal" bones of reptiles and mammals.

fishes are homologous organs ; nor as less so that the tegumentary spines of the Plagiostomes are homologous with their teeth, and thence with the teeth of all vertebrata. Again, it appears to me indubitable that the teeth and the hairs are homologous organs ; they are therefore either both enderonic or both ecderonic. Taking for granted the validity of a basement membrane as a mark of the boundary between ecderon and enderon, I elsewhere[1] arrived at the conclusion that the teeth are enderonic organs, and that therefore the hairs must follow them. Now, however, that a "basement membrane" turns out to be no test at all, there seems no reason why we should not be guided entirely by the direction of growth and consider both hairs and teeth as ecderonic organs; the former being a development of the cellular ecderon, and corresponding with the ordinary horny epidermis ; the latter, a development of a deep layer of the ecderon beneath this. It appears to me that we can do no other than admit this view for the teeth ; but if this be the case, we may apply it to the scales of fish (and the "dermal plates" of reptiles ?) also ; as there are no difficulties about the latter which are not also presented by the teeth.

There appear, in fact, to be but few objections of any importance to the assumption of the ecderonic nature of fish scales, the principal ones being the continuation of the tissue of the ecderon over the upper surface of the scales ; the apparent passage of the bony structure into the laminæ of the connective tissue of the enderon below, and the vascularity of the latter.

The continuity of the enderon over the scales will be seen below to be more apparent than real. I have not been able entirely to satisfy myself, as to the exact relations of the parts, in the case of the eel, but in the other fishes which I have examined the surface of the scale is very partially covered by the enderon, being in its centre, at any rate, in contact with the cellular ecderon.

The vascularity of the scale never extends to its most superficial layers, and may be explained in the same way as that of the test of an Ascidian, which however is unquestionably an ecderonic structure. The passage of its deep layers directly into the connective bundles of the enderon, which Leydig has observed in Polypterus (and which I will not say does not occur elsewhere, though I have not observed it), would appear to me only to indicate that this scale, and perhaps others, are composed of two portions, a superficial ecderonic part

[1] On the Structure and Development of the Teeth, *Quarterly Journal of Micros. Science*, 1852.

extending as far as the most superficial vascular canals, and a deep portion beneath these belonging to the enderon.

However, all these points can only be decided by a much more extensive series of investigations, principally directed to the ascertainment of the position of the protomorphic line and of the direction of growth of the constituents of every scale, than I have hitherto had time or opportunity to carry out; and as the attention of other observers does not appear to have been directed to these particular points, the question must for the present remain undecided.

Professor Williamson in his valuable and philosophical contributions to our knowledge of this subject (Phil. Trans. 1849-1852) laid the foundation for a comprehension of the mode of development of fish-scales, by pointing out that Agassiz's views, though essentially true, yet require a certain modification. For though a fish scale does really grow by the apposition of layers to its deep surface, as Agassiz asserted, yet it is not included in a sac of the epidermis (if by that term we are to understand the ordinary cellular ecderon); and it is also true that its deeper portions grow by their superficial surface. Professor Williamson points out, in fact, that every fish-scale consists of at least two portions, a superficial homogenous, or at most canaliculated, laminated layer, the *ganoin* (so-called enamel or horny layer of authors), and a deeper, also laminated, frequently fibrous or osseous portion commonly traversed by Haversian canals. Now these two portions have a certain independence in their mode of growth, at any rate after their first formation, as may be easily understood by the accompanying diagram (*fig.* 307.), which represents a series of imaginary sections of scales from their first growth onwards; a, is the protomorphic plane; b, b'', the deep ecderon; b', the superficial cellular ecderon, and the line x, the centre of the scales from which development commenced.

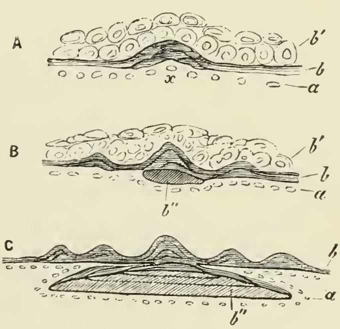


Fig. 307.

Suppose A to be the youngest scale, constituted merely by a thickening and calcification of the deep ecderon, which in B has added several layers by apposition to its inner surface, all of which retain the ganoin structure except the deepest, which becomes fibrous in its texture, and forms the commencement of the "Lepidine" layers of the scale;—these layers, however, being as much a part of

the ecderon as the former. In C the scale widening, the edges of its "Lepidine" layer do not remain in contact with the ganoin layer; but it will be obvious that the re-entering angle thus formed by the protomorphic line between the two, is only, as it were, a fold of the deep surface. If the two layers go on increasing in this way, however, the ultimate effect will be that, although growing in reality by its deep surface as before, the "Lepidine" layer of the scale will appear to grow by its superficial surface, and that addition of layers to the upper surface of the scale observed by Professor Williamson, will take place. If the explanation here proposed, however, be correct, this will form no objection to, but a confirmation of, Agassiz' views.

It will be well, however, with this clue to turn from the theory to the facts of scale development.

All that I have observed leads me to confirm Professor Williamson's conclusion, that there is no real line of demarcation to be drawn between placoid, ganoid, ctenoid, and cycloid scales; all these forms passing into one another. Indeed, I conceive that the only method thoroughly to comprehend the cycloid and ctenoid scales is to examine, in the first place, the so-called placoid and ganoid forms.

Hermann Mayer and Leydig have shown (and the fact is readily verifiable) that the scales and spines of the Plagiostome fishes are formed by the gradual deposit of calcareous matter in processes of the integument, which are at first coated by the ordinary cellular ecderon. These diverticula, in fact, originally resemble other papillæ of the skin, and like them, are bounded by a structureless protomorphic layer, marking the boundary between the cellular ecderon and the enderon.

When the formation of the placoid scale commences, however, instead of the successive division and multiplication of the endoplasts and the cellulation of the periplast of the ecderon, which before went on, a deposit of calcareous matter takes place at the boundary-line, and the structureless band remains as structureless or "basement" membrane, investing the future spine. The deposit increases until the enderonic pulp occupies but a very small space, or even completely disappears, and the spine projects as a cylindrical or conical tubercle. When it has attained its full length, the deposit does not cease; new calcareous matter is continually added to its inner extremity, but rather in the direction of breadth than of length, so that, eventually, an irregular broad plate is formed with the spine projecting from its outer surface (*fig.* 308.).

It is particularly to be remarked, however, that the projecting

body of the spine being once formed, the calcareous additions which give origin to its base (*c*) gradually cease to be in exact apposition with the original protomorphic zone ; and in proportion as the base of the spine extends, have we a wider and wider interval, occupied by the tissue of the enderon, between its upper surface and the under surface of the ecderon (*f*). Examining it in the perfect state, then, it would appear that the spine is included in a sac of the enderon ; and this appearance is very much strengthened if dilute hydrochloric acid be added, by which the enamel layer (*a*) is dissolved out, and the structureless membrane enclosing the spine rendered distinct ; while its continuity with that structureless layer which bounds the enderon is at once obvious. From its development, however, it is clear that this is a simple appearance, and that the apparent sac results from the projection inwards of the extremity of this truly ecderonic structure. In fact, inasmuch as the base of the spine grows like its shaft by continual addition to its inner surface, while its apex is unquestionably an ecderonic structure, this base might be considered to be enveloped in an involution of the protomorphic plane of the ecderon (*fig*. 307. C).

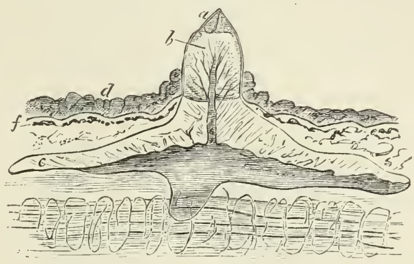


FIG. 308.

Now suppose such plates as these to have acquired their maximum in width and minimum in height ; furthermore, imagine them to be so closely set in the skin that the posterior edge of one over-rides the anterior edge of the one next behind it, and we have the exact arrangement of the scales in the cycloid and ctenoid fish (*fig*. 309.).[1]

A careful study of the scales of that remarkable animal the Sturgeon, which exhibits in this, as in so many other characters, its intermediate position between Teleostian and Plagiostome fishes, appears to me to throw still further light upon the difficulties of scale development.

The scales of the sturgeon are large, slightly convex, rhomboidal plates, set obliquely in the skin, so that, while the posterior two-thirds

[1] The flexible cycloid scale of the eel presents an exact parallel to the tooth-like placoid scale of the skate, except that it is flat instead of conical, and that, in the adult state, the scale appears to be completely included in the enderon, and is wholly covered by the cellular ecderon. I believe this appearance of inclusion in a complete sac to proceed simply from the smallness of the original point of contact of the scale with the cellular ecderon, and the rudimentary state in which the whole organ remains.

of their surface are bare and hard, the anterior third becomes gradually softer from the prolongation of the integument over it. The posterior surface continues hard up to its sharp edge, but it is supported below by a soft thick layer of integument, which passes on to the anterior soft coat of the scale behind, and thus masks the real overlapping of this scale by the posterior edge of that which precedes it (*fig.* 310. B).

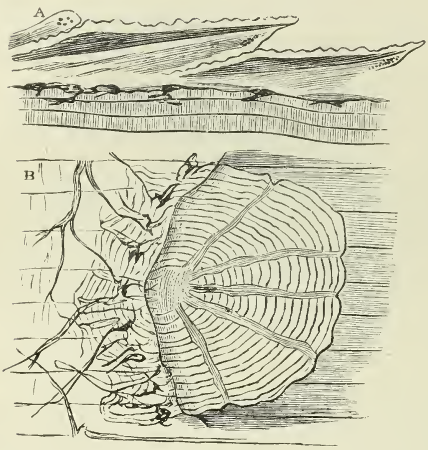


FIG. 309.—Scale of the Roach (*Leuciscus*). A, section ; B, surface.

The surface of the scale is shining and glassy. It is marked by a medium ridge, whence it shelves upon each side, and by an elegant sculpturing produced by raised, hard ridges of the same nature, which radiate from the margins centrally for about a fourth of the semidiameter of the scale. In the region within this zone, the ridges gradually lose their regularity, the radiating lines anastomosing with one another and forming an elegant polygonal network. The soft surface of the integument of the anterior portion of the scale, is raised into many minute papillæ (*fig.* 310. A, *a*), which may be followed for some distance on to the hard portion. Furthermore, it exhibits scattered round spots, with projecting centres of the same appearance as the ridges, and like them feeling hard to the touch.

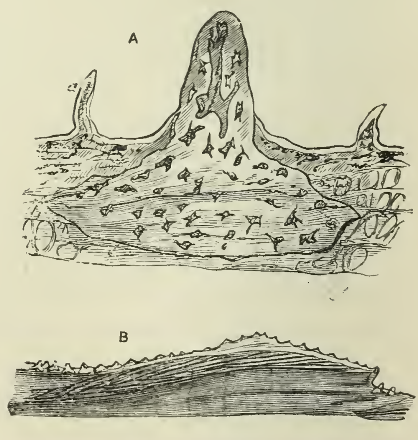


FIG. 310.—Scale of Sturgeon. A, one of the detached tubercles highly magnified ; B, the entire scale.

If a section of the scale be made (*fig.* 310. B), its under surface will be found to have a concavity corresponding with the convexity of the upper. If the section has passed through one of the ridges, it is seen that the osseous tissue of the scale is of two kinds : a superficial homogeneous-looking, dense, comparatively thin layer, and a deep, thick, laminated portion. If traced from the centre of the scale

to its anterior circumference the superficial layer loses its continuity, breaking up into conical bodies, which are the sections of the detached calcareous spots mentioned above ; the deep layer thins out, its laminæ gradually becoming fewer, and leaving a soft membranous space between their upper surface and the under surface of these spots. In the centre of the scale again, a series of rounded apertures are seen in a tangential section, the sections of canals which radiate through the scale and become more numerous and wider towards its margin. They are connected below with vertical canals passing through the laminated layer, and anteriorly they pass into the wide membranous space above referred to. There is no histological difference of any importance in the structure of these two layers ; each is composed of true bone with radiated corpuscles ; the upper being more dense and homogeneous, the lower less dense and laminated.

If a section be made through several of the ridges of the upper surface, it will be seen that they are entirely composed of the hard homogeneous osseous tissue. On their sides, however, and in the valleys between them, more or less of soft integument remains, whose pigment masses give the valleys a dotted appearance. On the other hand, a section of one of the detached tubercles shows, except in its consisting of osseous tissue only, that it is identical with a single spine of the Skate (*fig.* 310. A). It appears to me, therefore, that there can be no doubt that the ganoid, overlapping scale of the sturgeon commences by an isolated placoid spine ; that other spines are developed around this, and their bases uniting, constitute a placoid scale, between whose elevations little valleys, bridged over by the soft integument, remain ; that to the base of such a plate as this, continual additions of osseous laminæ are made, the radiating Haversian canals being left between the first laminæ and the superficial plate ; and finally that, extending in size, the anterior face of this complex scale becomes over-ridden by the preceding one. Complicated as it may appear, it is obvious that all this structure results from the continued endogenous growth and union of the primary ecderonic calcareous deposits, which constitute, as it were, so many centres of ossification for the large scale. The final structure, however, is (if we leave out of consideration its histological character), to all intents and purposes, that of a cycloid scale ; and its mode of growth is identical with that of the large cycloid scale described by Prof. Williamson.

The increase of the scale is concentric : addition being made to its posterior, as well as to its anterior edge and surface ; the only

difference being, that in the latter case the development of the upper layer is less rapid than that of the lower, while in the former they are coincident ; that soft membranous separation therefore, which exists between the two layers anteriorly, is far less developed posteriorly ; and the soft continuation of the scale which is flat anteriorly, is inflected posteriorly ; the process of addition being otherwise the same. Suppose, now, that each detached calcareous centre of ossification as it is added to the posterior margin of the scale, instead of being flattened, were produced into a spine as in the rays, then it is perfectly clear that instead of a cycloid scale, the result would be a serrated ctenoid scale. And this appears to be exactly what takes place in the scales of the perch, according to Prof. Williamson's description.

From all this, I think, we arrive at Prof. Williamson's conclusion, that fish-scales are essentially tegumentary teeth ; that like the latter organs, they result not from the calcification of the cellular ecderon covering those folds of the integument, upon which they are developed and which correspond with the dental pulp, but by a calcareous deposit taking place beneath this, in what represents a deep layer of the ecderon ; finally that it is, for the present, an open question whether the deep layers of all scales are produced by a continuation of this process, or whether in some cases a deep truly enderonic structure may be added to this superficial ecderonic constituent to constitute the perfect scale. A process of the latter kind would, at any rate, find its parallel in the eventual union of the teeth of many fishes with their jaws, and in that of the plates of the chelonia with the vertebral elements.

§ 3. *Histology of the tegumentary organs.*—Having thus arrived at a general idea of the mode in which the various forms of integumentary organs are produced from the primary morphological constituents of every integument, we have now to consider their minute histological elements and the mode in which these proceed from the indifferent tissue of which all organs are primarily composed.

The tegumentary tissues, like all others, are produced by the metamorphosis of the periplast of the protomorphic or indifferent tissue from which they take their origin, the endoplasts, to all appearance, taking but little share in the metamorphic processes. The chemical metamorphosis of the periplast may be either into horny, chitinous, calcareous, or cellulose matter ; in form it may become fibrous, laminated, vacuolated, bony, prismatic, &c.

As a general rule, the endoplasts tend to disappear, *pari passu*, with the metamorphosis in form and composition of the periplast ; but

the differences presented by different tissues in this respect have given rise to the establishment of a distinction between what is called the process of *conversion* and that of *excretion*. For instance, in the development of a hair or of a nail, the elements of the protomorphic layer evidently pass, as such, into the perfect substance of these organs; the periplast simply becoming horny, and the endoplasts remaining for a long while, or even always, visible in the cornified tissue. This is therefore a process of "*conversion*" of the protomorphic tissue. On the other hand, the chitinous coat of the lower Annulosa and the shells of the lamellibranchiate and gasteropod Molluscs arise in a totally different manner. The elements of the protomorphic layer do not pass into them entire, but they are formed, like the cuticula of a plant, or like the dentine and enamel of the teeth, by the successive outgrowth of layers of the outer portion of the periplast. No endoplasts, therefore, are ever found in them, and there is no *conversion* of the protomorphic tissue, but a process of *excretion*.[1]

At first sight this distinction would appear to be very decided, and likely to afford a good ground for the formation of definite sub-divisions of the integumentary organs into classes. Unfortunately, it is often difficult in practice to assure oneself in what way a given tegumentary organ has been formed. While the presence of endoplasts in a metamorphosed tissue is good evidence of its having been developed by conversion, their absence is no proof that the tissue has been developed by excretion; inasmuch as it may simply be due to their very early disappearance. In fact, if any one affirm that the shell of a Unio or of a Crustacean, notwithstanding the impossibility of detecting endoplasts in its youngest laminæ, is in reality formed by the successive apposition of entire layers of the protomorphic tissue, in which the endoplasts disappear so early that they cannot be detected, it would be very difficult absolutely to disprove the assertion, though we might ask for evidence of its truth. Disbelieving in the doctrine of the special vital activity of the endoplasts, I confess the question does not seem to me to be of much importance, and I have only enlarged upon the subject because great weight has by high authorities been laid upon these distinctions. It appears to me that the processes of conversion and of excretion grade one into the other, and that no real subdivisions can be based upon the occurrence of either to the exclusion of the other. I will, however, take care to indicate what appear to me to be clear instances of each. I shall now proceed to consider the histological structure of the integuments of

[1] Using the word in the sense of "growth out," not in the common perverted signification of fluid transudation and hardening.

animals in the following order:—1. Hydroid and Actinoid Polypes and Beroidæ. 2. Annulosa, including the worms and Echinoderms. 3. Mollusca, including the Ascidians and Polyzoa. 4. Vertebrata.

1. *Hydroid and Actinoid polypes.*—In these animals the integument consists either of a simple cellular and vacuolated ecderon, or the outer layer of this is developed into a structureless coat, which may become thickened by repeated additions, and thus attain considerable dimensions. In the common Campanularia, for instance, the outer wall of the bud from which a polype is to arise consists, at first, of a mass of indifferent tissue. As development proceeds, the outer portion of the mass is converted into a structureless membrane, which becomes detached from the body of the polype through its whole extent, and constitutes the future *cell*, the subjacent ecderon taking on the ordinary cellular structure. On the pedicle the same process goes on to a less extent, the structureless layer becoming separated only at intervals, so that the pedicle acquires a ringed appearance.

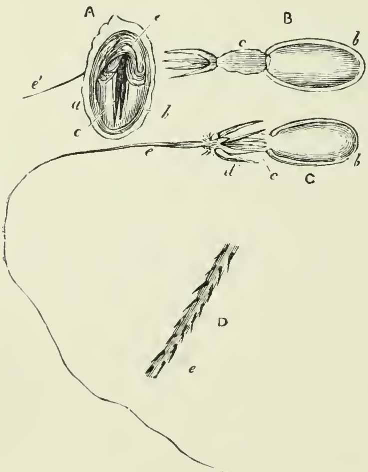


Fig. 311.

An integument of one or other of these descriptions is to be met with in all the Sertularian and Actinoid Polypes, and is obviously, in these cases, the result of a process of excretion. In the *Medusæ* and *Beroidæ*, on the other hand, where the integument is thick and gelatinous, the ecderonic tissue is converted, as a whole, into what closely resembles rudimentary connective tissue, in which elastic elements and muscular fibres are developed. The presence of peculiar organs, called the "*Thread or Urticating cells*," constitutes an extremely characteristic feature in the integument of these creatures. These (*fig.* 311.) are composed of a delicate membranous sac (*a*), enclosing a much thicker one (*b*), which is open at one extremity, the aperture being stopped by the end of a more or less irregular short stiff sheath (*c*), sometimes giving attachment to several distinct rays or spines (*d*), applied together, which is fixed to the edges of the aperture, and occupies the axis of the inner sac. To the extremity of this sheath a long, frequently toothed filament is attached (*e*), and lies coiled up round the central sheath, and in close contact with the walls of the

sac. The latter are very elastic, and seem to be tensely stretched by the contained fluid during life; for on pressure, the sac suddenly bursts, and its contents are evacuated so rapidly as hardly to allow of the process being traced. I believe, however, that the long filament is pushed out by the side or through the axis of the central sheath, remaining still firmly attached to the latter, so that the result is the appearance exhibited in the accompanying figure (*c*), where the sac is seen empty, the long serrated filament being attached to the sheath, which, everted and with its spines spread out, is itself fixed to the margins of the aperture. The violent protrusions of these minute serrated filaments, aided, perhaps, by some acidity of the liquid of the sac, is in the larger kinds, such as those which exist in Physalia, exceedingly irritating to the human skin, and usually proves fatal to the minute creatures on which the Hydrozoic and Anthozoic polypes prey.

Integument of the Annulosa. — The integument of the lower Annulose tribes, of young forms and of the more delicate parts of a great majority of the higher Annulosa, consists of a thin structureless chitinous membrane developed from the subjacent cellular ecderon, in a manner essentially similar to what has been described in the Polypes.

Leydig has particularly described this form of integument in Entomostracous Crustaceans, (Branchipus and Argulus) in insect larvæ, (Corethra), and among the Annelids in Piscicola, Nephelis, Hæmopis, Sanguisuga, Clepsine and Lumbricus, where the integument consists of two portions—a deep cellular layer and a superficial layer, which is either absolutely structureless, or is fibrillated; being in no case formed by the coalescence of the subjacent cells, but by excretion from them.

A similar structureless excreted integument is found also in Planariæ, Nemertidæ, in many Cestoidia, Nematoidea and Trematoda, and, according to the late researches of Leydig, on Synapta, in the Echinoderms also. Where the integument is not very thin, and consists of several layers of chitinous matter, the added laminæ commonly take on a fibrous structure. The Nematoid worms present particularly good examples of this complication. Thus, for instance, the integument of Mermis albicans, which has lately been examined with much care by Dr. Meissner, consists of three layers, the middle of which is double. The outermost of these layers is either structureless or presents a distinction into transverse hexagonal plates, each of which occupies $\frac{1}{6}$ of the circumference of the animal. At the head and tail, small polygonal plate-like markings replace these, and such

small plates could be detected, making up the large ones. Dr. Meissner calls them "cells," but expressly states that he never detected any nucleus in them, and it seems more probable that they are produced by modifications of the original external structureless layer, similar to those which, as will be seen, occur in the Crustacea and Mollusca.

The middle substance of this integument is composed of two layers of fibres one above the other. The fibres are parallel in the same layer, but those of the two layers cross one another at right angles, so that they form two sets of opposite spirals. The fibres are sharply contoured, dense, and brittle, and those of each layer are divided into six sets, corresponding with the six sections of the body. At the sutures the fibres of each bend back upon themselves, and run in a parallel course to the opposite suture.

The deep layer is the thickest ; it appears longitudinally striated on section, and may be split into lamellæ of any thickness ; otherwise it is perfectly structureless.

In the Nemertidæ, according to the researches of Quatrefages, the integument has essentially the same structure, consisting of a superficial structureless ciliated lamina, with deeper vacuolated and fibrillated layers. In the other Turbellaria the vacuolated structure is predominant.

This fibrous chitinous integument is still better developed in the Insecta.

According to Mayer (*l. c.*) the chitinous integument of Lucanus cervus is composed of glassy rods with sharply defined dark, parallel edges, which by their mutual apposition and anastomosis, and probably by the interposition of a connecting mass, form thin layers. The rods in each layer are parallel, but those of different layers cross one another at angles of from 45° to 90° ; so that a horizontal section presents a sort of elegant cross-hatching, the lines of which are about 0·008 mm. apart. The outer surface of this laminated mass is invested by a transparent homogeneous substance containing pigment, and above this by a layer of epidermic "cells" (0·005 to 0·01 mm. in diameter), with nuclei and nucleoli, their edges being separated by an intermediate substance. Internally, there is also a layer of epidermic "cells" which are polygonal from mutual pressure. They are without nuclei, but possess a short spine, arising from the centre of the cell, and ending by a sharp point. Quekett (*l. c.*) describes a similar structure, consisting of striated laminæ, in the integument of Dynastes Hercules.

The integument thus described closely resembles that of the

larger Crustacea (*vide infra*), and I should have placed it with them, except for the very distinct statement of Mr. Newport with regard to the development of the integument in Melöe. According to Mr. Newport's researches, the integument of the young Melöe is at first composed of polygonal nucleated cells, the largest of which is about $\frac{1}{2000}$ of an inch in diameter. As the animal grows, the nuclei divide and subdivide by a process of fission, and the integument becomes composed of several layers. After awhile, the deeper of these undergo a fibrous metamorphosis, and constitute a fibro-cellular structure, which gives attachment internally to the muscles, while the external layers continue to grow, and to be reproduced as distinct cells.

If this were the mode of development which obtained in all Insecta we must consider their chitinous integument to be produced by conversion of the previously existing cells of the ecderon. However, Leydig's statements are equally decided, that the integument of Corethra presents no appearance of cellular origin, and the question may, therefore, for the present, probably be considered undecided.

The calcified integument of the Crustacea presents the same general structure as that of the other Annulosa, consisting of superposed chitinous, more or less fibrous lamellæ, the outer of which are infiltrated with a calcareous deposit. In the small transparent Crustacea, as we have already seen, the integument is composed of structureless layers, developed by excretion on the surface of the ecderon, and even in the largest forms, the minute hairs, &c., present precisely the same appearance; but in the thick integument of the Decapoda, certain layers of the shell have been described, not without considerable show of reason, as possessing a cellular organisation (Carpenter).

I have carefully examined the shell of the common crab in relation to this point, and the following are the results of my investigation.

It appeared to me in the first place, that, without seeking for a moulting crab, the structure of the integument in its uncalcified state might be readily ascertained by examining the soft membrane connecting the articulations of the limbs which, as is well known, is continuous on either hand with the calcareous integument, and passes into it. In a section of this soft layer (*fig.* 312. A), I found from within, outward, 1. The enderon (*a*) composed of connective tissue, excavated by vascular channels, and containing numerous aggregations of pink and yellow pigment, frequently disposed in a stellate form, or even forming anastomosing net-works along the rudimentary elastic fibres of the tissue. 2. The surface of this (*b*) was constituted

by a protomorphic layer consisting of a homogeneous substance containing endoplasts (C), which sometimes adhered to the enderon, sometimes to the hard integument, when the latter was detached. 3. Superficial to this, was the chitinous layer of the integument (c) composed of a number of laminæ of great delicacy, and not more than $\frac{1}{3000}$ of an inch apart. The deep laminæ were much softer than the superficial, and the outermost lamina of all was hardest, and of a brownish colour, constituting the structureless epidermis of Carpenter and Lavalle.

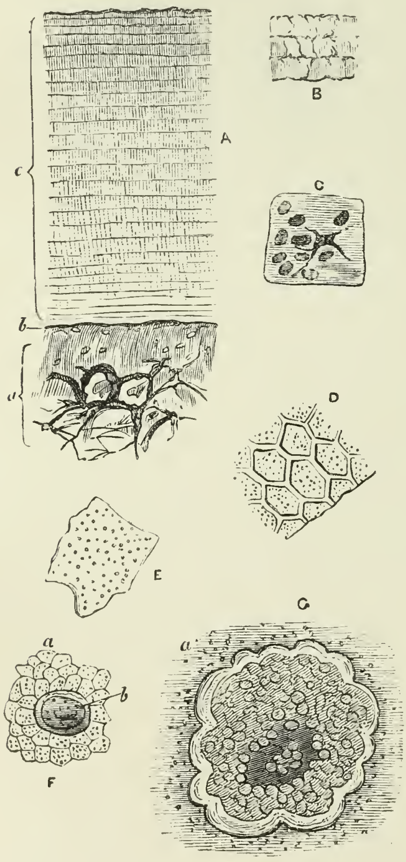


FIG. 312.—A to E, from the crab; F, G, from the shrimp.

In section, the deep laminæ (B) presented only an indication of perpendicular fibrillation; but this became more marked superficially, the outer part of the section appearing closely striated. The deep laminæ, when stripped off, presented no definite structure, but they readily fell into plaits; while the superficial laminæ appeared dotted over. I sought in vain for any appearance of endoplasts in the deep layer, where, however, had they existed, they must have been readily detected; and I therefore conclude, that the chitinous lamellæ are formed from the subjacent ecderon, by a process of excretion. It should be remarked, however, that a minute polygonal areolation is observable at times upon the most superficial "epidermic" layer. I do not know from what cause this proceeds, but the areolæ are certainly not cells.

Such is the structure of the soft interarticular integument, in which I could find no calcareous matter. If it be traced into the hard calcified shell, the only alteration observable is, that a dark calcareous deposit takes place, the earthy matter being infiltrated, as it were, through the laminæ. The deposit affects, however, only the middle layers, the extreme outermost being left as the "horny epiderm"; while a

variable number of the inner laminæ remain as a more or less thick soft coating upon the inner surface. These soft layers may be stripped off as a parchment-like membrane, with the muscles, and their relations to the enderon are then readily examined. They are here as structureless as where they constitute the deep layer of the inter-articular membranes.

The structure of the calcified layer has been carefully described by Dr. Carpenter, who showed, that in the crab and lobster they are traversed by tubules identical with those of dentine, and pointed out the error of Lavalle in regarding these as fibres. There can, I think, be no doubt, that in the crab and lobster, Dr. Carpenter's doctrine is correct ; but I am equally of opinion, that for other crustacea, such as the shrimp, M. Lavalle is right. I believe, in fact, that the tubular structure is produced by the horizontal lamination giving way, as the calcareous matter is deposited, to perpendicular fibrillation of the chitinous matrix, and that, eventually, the uncalcified fibrils disappear and leave tubules in their place. That at least appears to be a natural conclusion from the fact, that the perpendicular fibrillation of the soft tissue becomes more and more marked externally ; and thus, by decalcifying the calcified shell, we obtain horizontal separable laminæ composed of short perpendicular fibres.

The colouring matter has always appeared to me to be generally diffused through the upper layer, and not to be confined to what Dr. Carpenter describes as the " cellular layer." The latter is a very thin stratum, made up of only a few of the superficial laminæ, which I have found to be most readily observable by detaching with a sharp knife a very thin scale from the upper surface of the crab shell. It is composed, exactly as Dr. Carpenter has figured it, of regularly polygonal, often six-sided areæ, frequently presenting a darker radiating patch in the centre, and, at first sight, irresistibly suggesting a true cellular structure.

I believe, however, that it is in reality nothing of the kind, but that, like similar appearances in the molluscan shell, this is simply the result of the concretionary manner in which the calcareous matter is deposited. We have seen, in fact, that there are no such appearances in the deep uncalcified layers, nor in the thin layers which invest the minute transparent appendages—considerations which appear to me to be in themselves decisive against the cellular nature of these bodies. In addition, decalcification brings to light no endoplasts in the " cells," but in their place we observe clear polygonal spaces in the membrane (*fig.* 312. D) which present the same dots (section of tubules) as those which exist in the simply laminated portion of the

integument (*fig.* 312. E). Finally, if the decalcified scale include a sufficient number of layers, it is easy, by altering the focus of the microscope, to trace the areolation inwards, until it becomes gradually fainter, and disappears, passing into the ordinary dotted laminæ.

I believe, then, that the "cellular" layer results from a peculiar additional deposit of calcareous matter in the uppermost layers of the shell; and this view is strikingly confirmed by what may be observed in the shrimp. The integument in this crustacean (*e.g.* the carapace) has exactly the same general structure as that of the crab, consisting of hard upper and soft deep layers, which are dotted and striated, and not tubular. The former owe their hardness to a generally diffused, transparent, calcareous deposit, which allows the previous dotted structure of the laminæ to be perfectly obvious. In some parts and in the superficial layers, this deposit is structureless and homogeneous (*fig.* 312. G, *a*), but in other parts the youngest layer presents very delicate polygonal meshes, whose areæ were about $\frac{1}{1000}$ in. in diameter (*fig.* 312. F, *a*). Decalcification completely destroys this appearance; so that I imagine it to be caused merely by the mode in which the primary deposit in the membrane takes place, the areolæ becoming almost immediately fused together by further deposit.

Through these homogeneous hardened outer layers thus constituted, there are dispersed more opaque spots (*fig.* 312. F, G, *b*), more or less rounded in their outline, and varying in diameter from $\frac{1}{500}$ in. or less, to ten times that size. The smallest of these bodies have exactly the appearance of cells (*fig.* 312. F, *b*), consisting of a dark centre, with a circular more transparent wall, and every variety of form may be observed between these and large masses, such as that figured (*fig.* 312. G, *b*), with a lobulated laminated circumference, and an irregular centre, composed of small masses like dentine globules. In the former the dots of the original tissue may be still seen; but in the latter they are not traceable and seem to be obliterated. If dilute hydrochloric acid be added while the object is still under the microscope, however, these bodies are gradually dissolved out with effervescence, and the structure of the place they occupied is found to be identical with that of the other portions of the integument. They are, therefore, nothing but concretions of calcareous matter, whose deposit has taken place in a peculiar form, quite independently of the primary structure of the part; this form being, in the smaller concretions, most deceptively cell-like. It appears to me that this case, in which the assumption of structure without cell development may be so plainly demonstrated, has a most important application, not only to the mode of formation of

Crustacean and Molluscan shells (*vide infra*), but to the development of the teeth, strongly confirming, I think, the view which I have taken of that process.

Integument of the Mollusca.—The soft surface of the body of the Mollusca in general is constituted by an ordinary, commonly ciliated, cellular ecderon, which needs no special description. The hard or soft shells which so many of them possess, arise in two modes; the calcareous and horny integumentary appendages being, I believe, invariably produced by *excretion*, while the Ascidian test, which contains cellulose, is formed by *conversion*. It will be advisable to treat of the structure and histological development of these two forms separately; and, first, of the

Excretionary integument of the Mollusca.—This is to be met with in its simplest form in the Polyzoa, in which the integument (ectocyst of Allman) is formed by a structureless membrane containing imbedded calcareous or silicious particles.[1]

An admirable example of the calcareous integument formed by *excretion* is to be found in the shell of Unio and Anodon.' The outer surface of the shell in these Lamellibranchs is, as is well known, covered by a brownish or greenish irregular membranous substance, the so-called "epidermis" of the shell. This substance, however, by no means constitutes a single membrane; on the other hand, the surface of the shell is marked by an immense number of closely set, more or less parallel, concentric lines, some of which appear to be formed by rugæ of the "epiderm," while others are the free edges of epidermic laminæ cropping out under those of older date. Viewing this surface of the shell by transmitted light with a low power, a number of polygonal closely set areæ come into view on depressing the focus through the thickness of the epiderm.

The inner surface of the shell has, for the greater part of its extent, a pearly or nacreous lustre; but along the gape of the shell, at a distance of from less than one line, to as much as two or three lines, from the free edge, the nacreous appearance ceases, and we find, instead, a brownish hue similar to that of the epiderm, and becoming gradually more intense till the very margin is constituted by a flexible brown membrane continuous and identical with the epiderm on the exterior. If the surface of the flexible zone be examined as before, its outermost portion appears quite homogeneous; as we pass gradually inwards, however, dots appear in it, and the hard portion of the brown zone presents polygonal areæ, precisely

[1] I am indebted to Mr. Busk, whose extensive researches on these animals are well known, for the information on which this statement is based.

resembling those under the epiderm on the outer surface. Where the nacreous appearance commences, these areæ disappear, becoming obscured by an opaque white substance, which is marked by elevations and depressions, corresponding with, though less prominent than, the principal ones upon the external surface.

If, now, a section perpendicular to the surface and to the concentric lines be taken, and viewed in the same way by reflected light, the cause of the various appearances which have been described will become obvious.

It will be seen that the thick middle of the shell is composed of three substances; of a very thin external brown layer, the "epidermis," and of two other layers more or less equal in thickness; an external, composed of minute polygonal prisms or columns set perpendicularly to the surface, and an internal, which looks structureless, with a fracture like loaf sugar. The outer prismatic layer preserves its thickness as far as the "brown zone" above described, and then gradually thins out into the flexible marginal membrane. The inner nacreous layer, on the contrary, gradually thins out, and ceases at the commencement of the brown zone. The ends of the prisms are, therefore, bare in the brown zone, whence the polygonal areolation observed in it; while its colour arises partly from the brown epidermis shining through, partly from a slight tinge of the same kind which runs through the prismatic substance, and renders it distinguishable, even to the naked eye, from the intensely white nacreous layer.

Thin vertical sections of these shells present the following appearances under a high magnifying power. The external edge is constituted by a delicate brown band, the "epidermis," in which no structure of any kind can be detected. Within this is the prismatic layer, a dense transparent substance marked by strong parallel lines which run perpendicularly to the surface and either extend completely through the layer, or terminate by joining some other within it. In the former case, the spaces which they enclose appear like the sections of prisms (of $\frac{1}{200}$ of an inch, more or less, in diameter): in the latter, they resemble longer or shorter cones whose bases are turned outwards. A number of such short cones are usually interposed between those ends of the prisms which are in contact with the epidermis.

Internally, or at the line of contact of the prismatic with the nacreous layer, the lines either remain parallel or converge.

The prisms are readily broken away from one another, and in this case, or in a sufficiently thin section of the whole layer, they are seen to be traversed by very closely set parallel transverse lines about

$\frac{1}{10000}$ in. apart. Each prism, however, does not possess a set of striæ peculiar to itself; on the other hand, the parallel lines stretch without interruption through the whole length of the prismatic layer, as if the prisms were not there. A horizontal section of the prismatic layer presents, as has been said, a coarse polygonal reticulation corresponding with the lines of contact of the prisms. The substance of the latter appears granular, but without any other structure in fully formed portions (*fig.* 313. A).

When a section of the prismatic substance is acted upon by dilute acid, the calcareous matter is extracted, and a membranous framework is left, presenting all the structural characteristics of the original tissue, except that the prisms are now hollow, and from their transverse striations have been well compared by Dr. Carpenter to the scalariform ducts of plants. This membranous residuum readily tears up into laminæ, each of which corresponds, usually, to a number of the fine horizontal striæ.

The white nacreous substance—*membranous shell substance* of Dr. Carpenter—which constitutes the interior of the shell, presents, in a vertical section, a horizontally striated appearance identical with that of the prismatic layer, and when macerated in acid it breaks up into corresponding laminæ. In fact, if we leave out the vertical markings which give rise to the appearance of prisms in the latter, the two structures are identical. This point appears to me to have been overlooked and to have given rise to the impression that there is a much greater histological difference between the prismatic and membranous substances, than really exists. The examination of the line of junction of the two substances (*fig.* 313. B), however will at once show their fundamental identity. The ends of some of the prisms will be seen in fact to project beyond the others into the membranous substance ; but it will be observed that the horizontal lines of the latter pass without interruption through the prisms, and therefore that the laminæ of the two structures are identical.

If we reduce these facts to their simplest expression, it will result that these shells are *composed throughout of superficial thin membranous laminæ, the outermost of which remains as epidermis, while the inner receive a deposit of calcareous salts.* Next comes the question, however, how are the structural differences between the prismatic and membranous layers produced.

Dr. Carpenter, in his well-known Essay, propounded the doctrine that both varieties of shell structure are the result of the development and coalescence of cells supplied by the mantle of the mollusk ; these cells remaining permanently distinguishable and coalescing in

rows, in the prismatic structure, but bursting and becoming confused into a homogeneous tissue, in the membranous substance. Nor, indeed, would it have been very easy in 1848 to arrive at any other conclusion than this, to which so great a number of appearances at first sight tend. Enabled, however, by Dr. Carpenter's great kindness and liberality to form my own judgment from his beautiful preparations, and having also worked over the fresh shells for myself, I have come to very different conclusions. I will not say that occasionally cells may not be enclosed in shell, but I believe I am in a position to show that, as a rule, shell-growth is not a case of *conversion*, but one of *excretion*, cells not being in any way directly concerned in the matter.

We may consider, first, the growth of the shell as a whole; and, secondly, that of its three constituents. Inasmuch as we know, that the shell of the young Unio or Anodon was once as thin as, or thinner than, the "epidermis" of the adult shell, and smaller than the smallest area, bounded by a concentric line on its outer surface; further, since we know that no addition is made to the outer surface of the shell directly; it is clear that the shell must grow in size by addition to its margin; in thickness, by addition to its under surface. Furthermore, since the extreme margin of any shell is constituted by the horny "epiderm," internal to which is the gradually thickening layer of prismatic substance, constituting the brown zone within which again is the white nacreous area, formed by the superposition of membranous layers over the fully-formed thick prismatic substance; from all this it appears to be equally certain that any given spot of the mantle of a young bivalve must give origin, directly or indirectly, first, to "epiderm"; secondly, to prismatic substance; and, thirdly, to nacreous substance; so that, on examining the free edge of a growing shell, we ought, since the "epiderm" is structureless and transparent, to be able to observe the gradual formation of the prismatic substance upon its under surface. This is, in fact, the case. *Fig.* 313, A, represents such a free edge of the shell of Anodon, *a* being the direction of the flexible zone; *b*, that of the perfect prismatic substance.

Dr. Carpenter describes the appearances here figured in the following terms (*l. c.* p. 8.):

"Although the prismatic cellular structure has not yet been actually observed in process of formation, yet certain appearances, which are occasionally met with in the marginal portions of its newest layers, throw great light upon its mode of growth, and indicate its strong resemblance to cartilage in this respect; for in these situations

we find the cells neither in contact with each other, nor polygonal in form, but separated by a greater or less amount of intercellular substance, and presenting a rounded, instead of an angular form (*fig.* 314. C). Upon looking still nearer the margin, the cells are seen to be yet smaller and more separated by intercellular substance, and not unfrequently we lose all trace of distinct cells, the intercellular substance presenting itself alone, but containing cytoblasts scattered through it. This appearance has been noticed by myself in *Pinna* and *Unio*, and by Mr. Bowerbank in *Ostrea;* so that I have no doubt that it is general in this situation. We may, I think, conclude from it that the cells of the prismatic cellular substance are developed, like those of cartilage, in the midst of an intercellular substance, which at first separates them from each other, that as they grow and draw into themselves the carbonate of lime poured out from the subjacent surface, they approach each other more and more nearly; and that, as they attain their full development, their sides press against each other, so that the cells acquire a polygonal form, and the intercellular substance disappears."

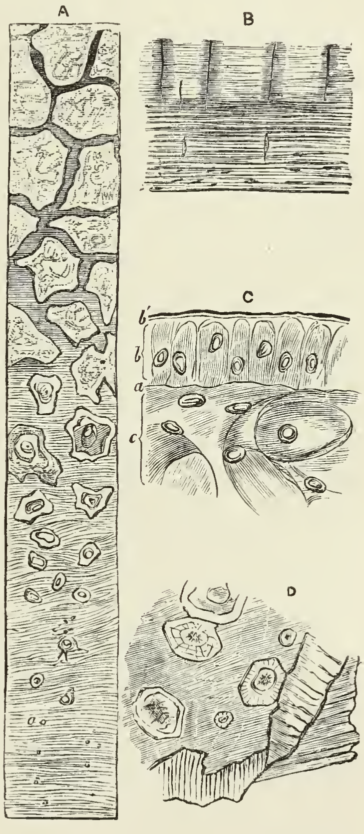


FIG. 313.—A to C, Unio; D, Helix.

I have given Dr. Carpenter's statement at length, because it appears to me to express very distinctly the interpretation which one is at once tempted to put upon the appearance, but which I must reject for the following reasons:—In the first place, if we examine that portion (*a*) of the margin beyond the smallest granules (*cytoblasts*, Carpenter), it is seen to be either absolutely structureless or obscurely striated, not a trace of a cell or endoplast being anywhere visible. Secondly, if any dilute acid be added under the microscope, the apparent nuclei and cells vanish with effervescence, and leave behind them clear empty spaces, of exactly the same shape and size as they themselves had. Thirdly, the supposed cells have a peculiar concen-

trically or radially-striated structure, resembling sections of urinary calculi on a small scale, and still more the corresponding bodies in the integument of the shrimp (*supra.*). For these reasons I think it must be granted that the appearances in question, however cell-like, are, in reality, not the expression of the development of a cellular structure at all, but merely that of the mode in which the deposit of calcareous matter takes place in the membranous basis of the shell. In fact, I believe that the calcareous matter appears first in small and distinct globules (the " cytoblasts "), and that more or less concentric deposits take place round these, the result of which is, that the membranous basis is more and more displaced, and that the deposited masses eventually come almost into contact. The regularity of the ultimate prismatic structure results from that of the distances of the granules primarily deposited, and the even rate of addition to each subsequently.

There appears to me to be but one interpretation to be placed upon these facts ; viz. that cells as such do not enter into the formation of the shell of the Naiades at all, but that it is constituted by the successive excretion of membranous laminæ from the surface of the epidermis of the mantle.[1] The outer laminæ retain their membranous nature, only becoming so far altered as to assume the horny aspect of the so called "epidermis" ; in the next laminæ, which are added to the inner surface of the young shell, calcareous matter is deposited in granules, additions to which are made in such a manner as to constitute the cellæform concretions, and ultimately, the process going on in the same way in successive layers, the prisms ; in the innermost laminæ, finally, the calcareous deposit results in an even, homogeneous, folded or striated layer. By scraping with a sharp knife the inner surface of the shell of Anodon, freshly detached from the mantle, I have obtained a distinct tough membranous layer, scattered through which were a vast number of close-set irregular granules of calcareous matter. A similar structureless layer without the granules constitutes the outermost surface of the ecderon of the mantle (*fig.* 313. C, *b'*) and may occasionally be detached as such. Such a layer consisting of the thickened outer portion of the periplast of the ecderon of the mantle is by no means an anomalous structure, as we have a formation of exactly the same kind in the "cuticle" of plants, and in the chitinous lining of the intestine in Insects ; and I believe that the shells of molluscs in general consist

[1] This is, after all, only a return to the opinion of Poli, whose observations on shell structure are remarkably accurate, and should never be overlooked. See his Testacea utriusque Siciliæ. Pars prima " in qua de Testarum natura atque affectionibus disputatur."

simply of a multitude of thin layers successively thrown off, superimposed and coherent, all the peculiarities of their structure arising from subsequent modifications, which are altogether independent of cells. This view is in perfect agreement with all that is known of the nature of the shells of larval Gasteropods and Acephala, which are invariably either of an absolutely structureless, thin, transparent, membranous character, or at most present a delicate striation. It may be added that not the slightest trace of a cellular structure is to be met with in the pellucid shells of the Heteropoda and Pteropoda. So much for the two primary forms of shell structure, the membranous and the prismatic. A most interesting variety of the former is the *nacreous* (mother-of-pearl) lining which is presented by many shells, both of Acephala and Cephalophora. The pearly iridescence proceeds, as Dr. Carpenter has well shown, from the folding of the membranous layer into close plaits, and not, as has been supposed, from the alternate cropping out of calcareous and membranous layers. Dr. Carpenter proved this by decalcifying with acid a layer of nacre from *Haliotis splendens*. The iridescence remained; but if the plaits of the layer were pulled out by stretching it with needles, the iridescence disappeared.

Another variety of structure usually, but not alone found in the membranous shell substance, is the *tubular*. "All the different forms of membranous shell structure are occasionally traversed by tubes which seem to commence from the inner surface of the shell, and to be distributed to its several layers. These tubes vary in size from about the $\frac{1}{20000}$ to the $\frac{1}{2000}$ of an inch, but their general diameter in the shells in which they most abound is about $\frac{1}{4500}$ of an inch. The direction and distribution of these tubes are extremely various in different shells; in general, when they exist in considerable numbers, they form a network which spreads itself out in each layer nearly parallel to its surface, so that a large part of it comes into focus at the same time in a section which passes in the plane of the lamina. From this network some branches proceed towards the nearer side of the section as if to join the network of another layer, whilst others dip downwards, as if for a similar purpose" (Carpenter, *l. c.* p. 14.). In other instances the tubes run obliquely through all the layers. The former structure was found by Dr. Carpenter in the outer yellow layer of *Anomia ephippium;* the outer layer of *Lima scabra* and in *Chama*, the latter in *Arca Pectunculus*, and *Trigonia*. In the latter case, the tubules are not continuous, but are seen under a high power to be formed by rows of isolated vacuities one for each lamina; corresponding, I imagine, with the appearance, "as if they

had arisen from the coalescence of lineally arranged cells," pointed out by Mr. Bowerbank and Dr. Carpenter. Having already given what are, I believe, sufficient reasons for denying the existence of cells of any kind in molluscan shells, I need hardly add that I cannot think this to be the true explanation of the mode of development of these tubules. In fact, I consider that the tubular shell structure is identical with that of dentine, and has precisely the same origin ; its tubuli arising not from cells, but like the canaliculi of bone, by a process of vacuolation in the calcified tissue. I regard the structure and mode of development of the Molluscan like that of the Annulose shell, in fact, as evidence of the strongest and most unmistakable kind in favour of the views with regard to the formation of dentine which I ventured to put forth in my essay "On the Development of the Teeth." Tooth and shell completely represent one another, structure for structure ; Nasmyth's membrane is the homologue of the "epidermis," the enamel that of the prismatic structure, the dentine, that of the membranous structure ; and all three are produced without the intervention of cells by the differentiation of primarily structureless laminæ. The existence of tubuli in the prismatic substance is not mentioned by Dr. Carpenter, but I have noticed them very distinctly in one of the sections of Pinna from his cabinet.

Finally in Rudistes and the sessile Cirrhopods, Dr. Carpenter has pointed out the existence of a peculiar *cancellated* structure "like that of Pinna on a large scale" only that the segments of the prisms are hollow instead of solid. These hollow prisms are covered externally and internally by a structureless layer.

To complete this view of the different varieties of shell structure, it may now be interesting to consider the mode in which they are combined in the shells of the various classes of the Mollusca. In the *Brachiopoda*, the calcareous shell is composed entirely of membranous laminæ, which are superimposed at a very acute angle with the surface of the shell, and are further remarkable for being thrown into sharp folds $\frac{1}{2000}$ to $\frac{1}{700}$ of an inch apart, perpendicular to their planes. In the great majority of the recent species again, all the layers of the shell but the outermost are perforated by canals ·0006 to ·0024 of an inch in diameter, each of which contains a cœcal process of the mantle, corresponding with those processes which we have seen into the cellulose tunic of the Ascidians ; the shells of *Lingula* and *Orbicula* are composed of horny laminæ perforated by oblique tubuli like those of dentine (Carpenter, *l. c.*). The shells of those families of Lamellibranchs, in which the lobes of the mantle are more or less united, are similarly composed almost entirely of laminated membranous shell

substance, *e.g.* *Mytilus*, *Modiolus*, *Tridacne*, *Isocardia*, *Conchaceæ* *Nymphaceæ*.

The tubular structure is met with in the *Arcaceæ*, in *Lithodomus*, in *Cardium*, and has generally a marked relation with the costations or sculpturing of the outer surface ; the membranous and prismatic structures are combined in the *Myaceæ* and *Solenaceæ*, and in those genera which have the lobes of the mantle disunited, as *Ostrea*, *Unio*, *Pinna*.

In the Gasteropoda the shell substance is invariably membranous, but the laminæ of which the shell is composed, usually three in number, are marked by parallel lines into rhomboidal bodies, which are described by Dr. Gray as crystals, by Messrs. Bowerbank and Carpenter as elongated, mutually adherent cells. I believe that neither of these expressions is exactly correct, but that these bodies have the same origin as the prisms of the lamellibranchiate shell ; a conviction in which I am strengthened by finding concentrically laminated bodies, like those of the Lamellibranchiates, upon the inner surface of the shell of *Helix* (*fig.* 313. D).

In *Patella* the middle layer is composed of perpendicular prisms, like those of Pinna. *Chiton* resembles it in this respect, but the outer layer is here composed of fibres parallel to the surface, and is pierced by short canals. In *Haliotis*, calcified plaited laminæ alternate with structureless horny layers, in immediate contact with which, says Dr. Carpenter, " is a thin layer of large cells of a very peculiar aspect." Dr. Carpenter considers that the plaited laminæ are cellular in this shell also.

Among the external shells of the Cephalopoda that of *Nautilus* has an external " cellular " layer as in Mya, and an internal nacreous layer like that of Haliotis.

The shells of all Lamellibranchiata, Brachiopoda, and of the majority of Gasteropod Cephalophora are external, being from their very origin never included in any involution of the mantle. It is different, however, with certain Cephalopoda and pulmonate Cephalophora, in which the shell commences its development as an internal organ covered over by the outermost layer of the mantle, and may either remain so enclosed during life (*e.g.* Sepia, Limax), or ultimately become naked as in Spirula and Clausilia. Although, however, these shells are truly internal (a distinction which, as I have endeavoured to show, carries with it some important conclusions),[1] yet the careful observations upon their development in Sepia by Kölliker, and in Clausilia by Gegenbaur, appear to furnish abundant evidence that they are still truly ecderonic structures, and that they bear the same

[1] See Memoir on the Morphology of the Cephalous Mollusca, Phil. Trans. 1852.

relation to ordinary shell as a nail bears to a horny epidermis among the higher animals. We know, in fact, that the nail, though to all intents and purposes mere cornified epidermis, is at first an internal structure, being covered over by the outer layers of the fœtal epiderm. A nail remaining so covered would correspond with the shell of Limax or Sepia, while an ordinary nail represents that of Clausilia. Gegenbaur, in fact, has shown that the shell of the latter mollusk commences at first like that of Limax by the deposition of a layer of calcareous particles in the midst of the cellular ecderon of the mantle beneath its outer layer of cells. The shell of Limax goes no further than this stage, while in Clausilia (and probably in Helix, &c.) it gradually increases by addition to its under surface, and finally bursts through the cellular investment which takes no share in its formation. It is the same with Sepia. Here the internal shell, or sepiostaire, is composed of two layers, a dorsal and a ventral; the former, according to Kölliker, is a thin membrane composed of slightly wavy, parallel, somewhat dark fibrils $0{\cdot}001\text{–}2''$ broad, which frequently appear to be composed of still more delicate fibrillæ. So far as this membrane corresponds with the ventral layer, it is covered on both surfaces by a thin structureless lamina of carbonate of lime, which has a pearly aspect on the ventral surface where it is not covered by the ventral layer; while it is granular on the dorsal surface, and on the ventral, where it is covered by the proper ventral layer, presents ridges to which the plates of the latter are attached. The thick ventral layer of the sepiostaire is composed of lamellæ set at a very oblique angle to the dorsal layer, and united together by close-set partitions at right angles to their surface. Acted upon by acid, this portion of the shell leaves behind it a membranous skeleton of exactly the same form, but presenting no further structure.

Young embryos present merely a fibrous rudiment of the dorsal layer. The ventral layer is formed by the successive deposit of calcareous laminæ inwards. When the first lamina has been formed, a deposition of small cylindrical bodies take place upon its inner surface. These increase, widen and become ramified at their extremities, forming ramified columns. A second calcareous lamina is now formed, connecting their ramified extremities, upon whose under surface the like process takes place, and this is repeated until the ventral layer has attained its full thickness. The ramified columns are regularly transversely striated; with the age of the shell additions are continually made to their lateral dimensions until they coalesce and constitute the septa of the perfect shell, upon which the striæ remain visible.

Kölliker was unable to find any cellular structure in the columns or laminæ themselves, but describes a layer of nucleated cells under the shell, which he regards as the agents in its secretion. Some researches recently made by H. Müller (Gegenbaur, Kölliker and H. Müller, *l. c.*) corroborate this view. He finds the shell of the Loligidæ invested by an excessively vascular membrane, which is almost wholly covered by a layer of epithelial cells towards the shell. On the dorsal surface they are for the most part rounded; on the abdominal surface, and particularly towards the anterior point, they form narrow cylinders which attain a length of as much as 0·07‴. They appear to give rise to the structureless layers of the shell. The lateral styles of the Octopods present similar relations.

The structure thus described, though apparently so widely different from that of ordinary molluscs, does not really differ very widely from the cancellated shell structure of Rudistes, &c., or still better of Pleurorhynchus as described by Dr. Carpenter. If we leave out the sides of the hollow prisms in the latter shell in fact, it will correspond exactly with one lamella of the ventral layer of the sepiostaire.

For a comparison of the shells of Spirula and Belemnites with those of Sepia and of Gasteropods, I must refer to Dr. Carpenter's Memoir so often cited.

2. *Conversionary integument of the Mollusca containing cellulose.*—This form of integument has hitherto been found in the Ascidians alone, in which the existence of cellulose was first detected by Schmidt in 1845. Schmidt's discovery was confirmed, the fact of the existence of cellulose in all the genera of Ascidians determined, and the chief morphological characters of their test set forth in the memoirs by Löwig and Kölliker " Sur les Enveloppes des Tuniciers," which appeared in 1846, since when further investigations have been made by Schacht and by myself. I must refer the reader to these papers for an account of the various opinions which have been entertained with regard to the structure of the Ascidian test, as I can only lay before him what are in my belief the facts of the case.

The test of the Ascidians is never composed of pure cellulose, but consists of an animal membranous matrix, to which the cellulose has the same relation as the calcareous salts have to the membranous basis of bone or of shell. The cellulose is, in fact, diffused through the membranous matrix, thoroughly impregnating it.

This membranous nitrogenous matrix in which the cellulose is deposited, presents great diversities of structure in the genera of Ascidians, representing, in fact, almost every known tissue. Thus in

one genus we have a test resembling cartilage ; in another, like bone ; in a third, like connective tissue. It may either be without vessels or traversed by branched and ramified vascular processes of the body. It is in all cases, however, a product of the metamorphosis of the ecderon of the outer tunic or mantle and, complicated as its structure may be, corresponds morphologically with the shell of other molluscs, or with the epidermis of the higher animals. In fact, if a section be made through the outer tunic and test of an Ascidian, as in *fig.* 314. A, taking care not to disturb the natural relations of the parts, we observe at the line of contact between the outer tunic and the test (*a*) an arrangement of the parts very closely resembling what exists at the junction of the derma with the rete Malpighii in the human skin. The outer tunic, like the former, is constituted by bundles of rudimentary connective tissue which run inwards to form sheaths around the muscles, leaving between them spaces, the sinuses of the blood vascular system, while externally they fuse together into a homogeneous substance containing endoplasts, which is thrown into processes and passes insensibly outwards into a layer of similar substance, with very close-set endoplasts almost perpendicular to its surface, which forms the commencement of the proper test. Externally to this rete Malpighii, the deposit of cellulose commences ; the tissue undergoing at the same time a fibrous metamorphosis. The line *a* is therefore a protomorphic line, and the test is the product of the growth and *conversion*, by deposit of cellulose within its elements, of a true ecderon.

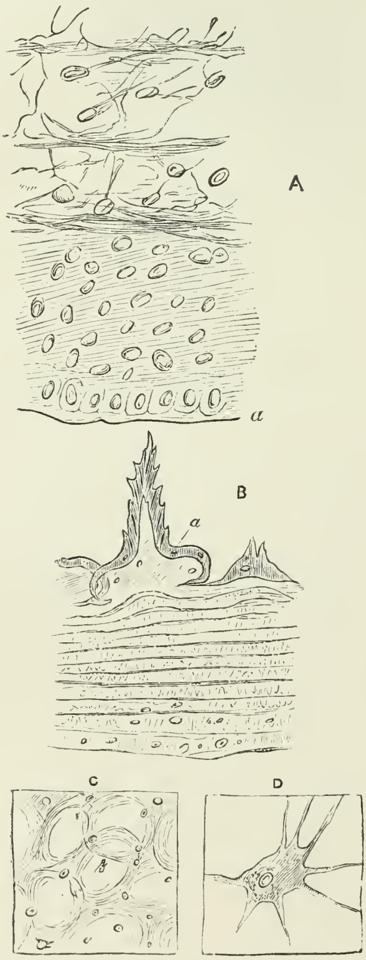


Fig. 314.

The separation of the ecderon (or test) from the enderon (outer tunic) takes place with great readiness in some Ascidians, as Phallusia, &c. ; while in others, such as Boltenia, many Cynthiæ, Salpæ, &c., it

can be effected with considerable difficulty, or not at all, and this difference has even been raised to the rank of a zoological distinction, the Ascidians having been in consequence divided into Monochitonida and Dichitonida. I believe, however, that in all those Ascidians whose test is unprovided with vessels, it is, normally, closely adherent to the outer tunic, and I am inclined to think that this is equally true even of those forms, such as the Phallusiæ, in which in preserved specimens the test and outer tunic are so commonly found detached from one another. Here, however, as the test is provided with an abundant vascular supply proceeding from one point of the body, it may normally become separated elsewhere. Careful examination of fresh specimens can alone decide this point.

The simplest form of Ascidian test is that presented by the Salpæ. Here, we have merely a gradual growth of the periplast and a deposit of cellulose within it, the endoplasts either remaining as such or becoming surrounded by cell walls. The resulting tissue, in fact, is identical with cartilage, if we suppose cellulose to have taken the place of chondrin.

In the Pyrosomata, the test has a structure which, on the one hand, resembles bone, on the other some forms of fibro-cartilage. The endoplasts, in fact, have become surrounded by cell walls, which are produced into long, frequently anastomosing processes (*fig.* 314. D); these retain their animal composition, while all the immediate tissue is strongly impregnated with cellulose. This is the fundamental structure of the test in the Phallusiæ and Clavelinæ also ; but here an additional complication results from the development in the substance of the test of a series of rounded cavities, which gradually enlarge until they almost come into contact, and give rise to a spongy texture. The intervening septa at the same time frequently become obscurely fibrous (*fig.* 314. *c*). Now these " vacuolæ," whose origin and nature appear to me to show their identity with the " cancelli " of bone developed from cartilage, have been described by Löwig and Kölliker, and by Schacht as cells ; and the latter has even stated that they possess a nitrogenous lining membrane. This is, however, a mistake, arising from the imperfect operation of the reagents by which the cellulose is detected ; it is simply less abundant close to the cavities of the vacuolæ, but may with care be demonstrated to exist up to their very edges.

Botryllus, Synöicum, Syntethys, Boltenia, and the Cynthiæ, present a new series of appearances : here the periplast of the ecderon is metamorphosed into fibres, which, however, are not composed of pure cellulose, but of a nitrogenous substance impregnated therewith,

In Synöicum the test is soft, and prevents very much the structure of some forms of rudimentary connective tissue. We find, in fact, a more or less distinctly fibrillated basis with scattered endoplasts; some of these are invested by round granulous nitrogenous cell-walls, while in others the cells are spindle-shaped and prolonged at each end into fibres (representing thus the elastic element of ordinary connective tissue), or they may be stellate. Botryllus, Syntethys, and Boltenia, present a similar structure, varying, however, in the extent to which the nitrogenous cell-walls on the one hand, and the periplast impregnated with cellulose on the other, have undergone development. Thus the periplast is broken up into very obvious fibres in Botryllus, while in Boltenia the fibrillation is pale and indistinct. On the other hand, I have nowhere met with so great a development of the nitrogenous cell-wall as in Synöicum.

In Boltenia a more or less distinct lamination makes its appearance in the test, and this peculiarity, as well as the fibrous structure altogether, attains its maximum in the Cynthiæ. In Cynthia papillata, for instance, the middle substance of the test is composed of numerous, very obvious laminæ, which consist of fibres directed alternately parallel with, and perpendicular to, the surface of the test (314. B.) At first sight, they appear as Löwig and Kölliker have described them, to be decussating sets of longitudinal and radiating; but on a careful examination of their sections I invariably found that the apparently radiating fibres bend round as they approach the apparently longitudinal set, and in fact pass into the latter. The longitudinal bands are, however, no thicker at one end of a section than at the other, so that the transverse fibrils cannot be merely given off from them. A transverse section, again, exhibits the same appearances as a longitudinal one; so that I think the fibres must in reality have a more or less regularly circular arrangement around the centre of the spaces occupied by the radiating bands, the apparently longitudinally fibrous bands arising merely from the decussation of these circular fibres. Great numbers of granular corpuscles (endoplasts?) are scattered through the midst of the "transversely fibrous" spaces. In Cynthia pomaria, Löwig and Kölliker describe peculiar "cells" in the inner layer of the test, consisting of such corpuscles surrounded by a thick circularly fibrous wall, and the existence of these bodies appears to be additional confirmation of the view I have taken as to the mode in which the fibres in Cynthia papillata are disposed. If in the latter, the fibres were disposed more closely around particular corpuscles, the test would, in fact, break up into just such circularly fibrous cells.

I have hitherto described only the structure of the middle, most

characteristic portion of the Ascidian test; it is next necessary to notice the inner and outer surfaces; the former of which is ordinarily said to be covered by a cellular epithelium, the latter by a more or less structureless horny epidermic layer.

The so-called epithelium is, I believe, in all cases merely the innermost unmetamorphosed layer of the ecderon, corresponding with the rete Malpighii of the "epidermis" of higher animals. As the Ascidian integument is ordinarily examined (*i.e.* in spirit specimens), it is in the condition of the macerated integument of one of the higher animals, and just as the "epidermis" of the latter may or may not, if stripped off, bring away with it the deepest layers of the *rete*, so the Ascidian test, when detached from the outer tissue, may or may not retain the corresponding structure.

The horny so-called "epidermis," on the other hand, is a structure well worthy of attention, as a similar element is, as we have already seen, to be met with in the widely different integuments of other Mollusca. In all Ascidians I have found the outermost surface to be formed by a structureless homogeneous layer, which contains less cellulose than the subjacent tissue, and often has a brownish horny aspect. In many Salpæ, Phallusiæ, and Cynthiæ, this outer layer constitutes merely a tough wrinkled investment. In others (Synöicum, Boltenia) it is prolonged with the subjacent layer into spines and processes, but without being much thickened. In other Bolteniæ again, and in various Cynthiæ, it is greatly thickened, and almost by itself constitutes large spines or even tesselated plates. In Cynthia papillata (*fig.* 314. B), the whole outer surface of the test is covered with spines (*a*), whose bases expand into polygonal plates, which strongly resemble the spines of the Rajidæ, to which reference will be made below. The brown substance here appears to have invaded the subjacent tissue, leaving spaces for the pre-existing endoplasts, so as to give rise to a structure precisely resembling the bone of the Plagiostomes, while to complete the resemblance, the pointed extremity of the spine is marked by lines which pass from its central cavity, parallel with one another, to the surface. I am not sure that there are tubes, but otherwise the appearance is exactly that presented by the pseudo-dentine of the integumentary spines of the skate.

It would appear, according to Milne Edwards, and the late observations of Krohn, that the rudiment of the mantle exists in the ovum of Phallusia before the cleavage of the yolk commences, as a structureless pellucid coat, containing solitary or aggregated greenish cells; and it would seem as if the outer structureless layer with which

we are at present concerned, arose from this coat, while the main thickness of the mantle is the product of the metamorphosis of the subsequently developed ecderon.

From all that has been said, I think it results that the Ascidian test is formed from the ecderon of the animal by a process of conversion which consists in the deposit, through its periplast, of cellulose, and a coincident morphological change which may result in the production of a tissue essentially resembling either cartilage, bone, connective tissue, or even dentine ; and that, therefore, an attentive study of the integument in this class alone is sufficient evidence that mere structure is no proof of the ecderonic or enderonic nature of any given organ.

Integument of the Vertebrata.—In these animals there are two classes of integumentary organs, differing in structure, chemical composition, and mode of development. These are, 1st, the *horny* and *glandular* tegumentary organs produced by the *conversion* of the cellular ecderon ; and 2nd, the *calcified* tegumentary organs which appear very frequently to be developed by a process of *excretion.*

1. *Conversionary horny organs.*—If a section be made of the integument of any mammal, it will be seen to be composed, leaving out of view its various appendages, of two principal portions, the enderon or derm, and the ecderon or epidermis. The latter, separated by a more or less distinct transparent line from the former, is internally composed of a homogeneous soft substance, in which are dispersed numerous oval or rounded endoplasts, set more or less perpendicularly to the surface of the enderon. Further outwards, they gradually become more distant and a cavity is developed round each, so that the ecderon becomes distinctly cellular. Still more externally the cellular periplast becomes changed in composition, being converted into a denser horny substance, and the change usually takes place so suddenly that the horny external portion (epidermis) is sharply marked off optically, and can be readily separated mechanically and chemically, from the internal unaltered soft portion, the *rete Malpighii.* The cell cavities at the same time become flattened, and by degrees almost obliterated, apparently by the pressure of the subjacent growing tissue ; but the endoplasts remain, and may always be detected if the horny layers are distended and rendered transparent, by the action of acids or alkalies. The horny stratum of the epidermis is therefore the result of the *conversion* of the walls or periplast of a whole layer of the cells of the ecderon into horn.

The hard structures of nails, hoofs, and horns (*i.e.* horny sheath of the horns of Ruminants) are developed in exactly the same manner ;

nor am I aware that any tissue enters into these organs, which is not entirely produced by the horny conversion of a cellular ecderon. The hoof of a fœtal lamb was entirely composed of such horny cells.

Structure of hairs, spines, and feathers.—In these tegumentary organs, we have to consider, first, their own proper structure, and, secondly, that of the sacs in which they are at first wholly, and always partially, enclosed.

The *shaft* of a hair is composed of three distinct structures, an external, the *cuticle;* a middle, the *cortex;* and an internal, the *medulla*.

The *cuticle* (*fig.* 315. C, D, E) on that portion of the shaft which lies within the hair sac, consists of two layers, while only the inner of them remains in the protruded portion. Viewed in section, as when a hair is observed in its totality, the cuticular layers form a thin double margin to the shaft, the outer (*b*) having the appearance of minute rhomboidal cells, joined end to end; the inner (*a*) seeming to be composed of close-set fibres arranged parallel to one another, and obliquely to the axis of the hair. If, however, the focus of the microscope be adjusted to the surface of the hair, or if the cuticular layer be detached from the shaft, these rhomboidal cells and parallel striæ are found to be the expression of irregular transparent structureless plates, overlapping one another, and closely united into tough membranes, to which their projecting edges give a striated appearance. No trace of endoplasts is visible in the older of these plates, and the matter of which they are composed is singularly unchangeable, remaining untouched on the addition of strong sulphuric acid, or of caustic potash, which completely dissolve the inner substance of the base of the shaft, and leave the cuticle in the form of a transparent, colourless, double membrane. In man, the outer layer of the cuticle ceases at the level of the sebaceous glands; and the edges of the plates of the inner layer lie very closely appressed to the shaft; in many of the lower animals, however, the plates are at a greater angle

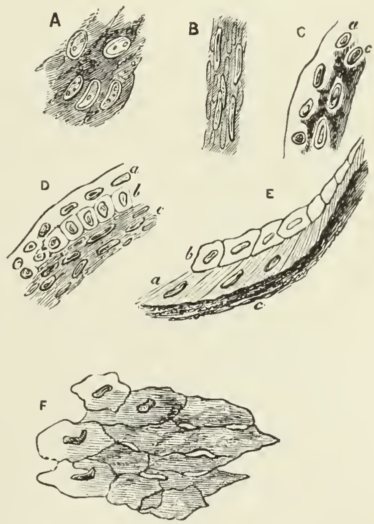


FIG. 315.—Hair, Man. A, B, D, E, F, from the nose; C, from the head.

to the axis of the hair, and their projecting edges give rise to the most elegant sculpturings of its surface.

The *cuticle* proceeds from the horny metamorphosis of the two outermost layers of the pulp of the hair. The lowest portion of the bulb of a hair, if viewed in section, presents a sharply defined edge (*fig.* 315., C), which may occasionally be raised up by reagents as a distinct structureless membrane ; but is normally perfectly continuous with the subjacent transparent homogeneous periplast of the pulp, in which lie the ordinary rounded or oval vesicular endoplasts of young indifferent tissue. Tracing the margin of the hair upwards, we find, next, that the two most superficial series of these endoplasts (D, *a*, *b*) are distinguished from the rest, by being free from that deposit of pigment granules which surrounds the endoplasts of the proper shaft substance ; and these two series are more or less distinctly contained in cavities or cells. The outer series is disposed more parallel, the inner more perpendicular to the surface. Still higher, (E) the cavities f the outer series are larger, and their party walls straight and sharply defined, while the endoplasts, which were at first plainly visible, disappear. In the inner series, both cavities and endoplasts disappear, and the periplast seems to split up into thin parallel horny plates (E), whose edges become more and more strongly marked. Such are the steps in the development of the cuticular layers which may be observed in short thick human hairs, such as those of the nostril. In those of the head, however, and in the hairs of the body of the calf, I have been unable to trace the cuticle into anything but a structureless layer, wrinkled externally, which passed into the superficial structureless layer of the deepest part of the bulb (C). I formerly thought that this indicated an important difference, but it is readily accounted for, if we suppose the process of development to be the same in each case, the endoplasts only disappearing very early in the latter.

The main substance of the rest of the shaft of all hairs, and its entirety in some, is composed of the *cortical tissue*. This is a horny hard substance, clear and homogeneous in white hairs, but filled with pigment granules, and moreover having its own special coloration in coloured hairs, which may be broken up mechanically, or by the action of strong alkalies and acids, into long, pale, sometimes striated fibres, which may or may not present remains of elongated endoplasts. Besides the latter and the pigment granules, a multitude of striæ and dots are visible in the cortical substance, which are produced by canals and cavities containing air.

The cortical substance results from the metamorphosis of the corresponding portion of the hair bulb. The primarily rounded

vesicular endoplasts (*fig.* 315. A), become greatly elongated and spindle-shaped, without ever, so far as I have been able to observe, becoming surrounded by a distinct cell cavity or wall (*fig.* 315. B). At the same time pigment granules arise in the periplast; it acquires a fibrous appearance, becomes horny, and splits up more and more readily into plates and fibres in the direction of its length. As it attains its perfect structure, rounded and elongated vacuolæ, which there is no reason whatever to suppose result from confluent cell cavities, arise in it and become filled with air. In fact the perfect cortical substance is a sort of rudimentary horny dentine.

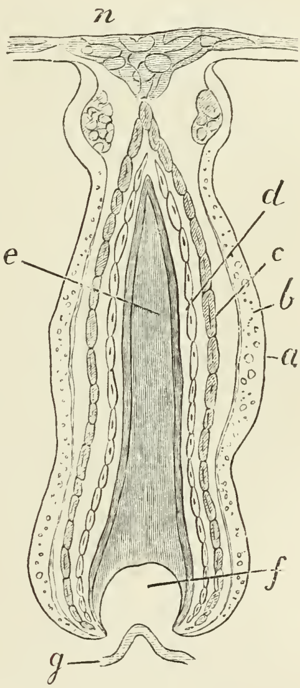


FIG. 316.—Diagram illustrative of the position of the different layers of the hair sac in a young hair. *a*, *b*, outer rootsheath; *c*, fenestrated rootsheath; *d*, imperforate rootsheath.

Lastly, the *medullary substance*—which contains a considerable development in the short thick hairs of man, and in those of the body of many mammals, but is frequently absent, as in the hair of the head of man, and according to Brücke (Reichert's "Bericht," 1849) in the bristles of the pig, the whiskers of the dog, seal, walrus and the long hairs of Myrmecophaga jubata—consists of a horny matter like that of the cortex and continuous with it, excavated into polygonal cavities, which frequently contain air bubbles and pigment granules. The cavities communicate, and the air may be driven from one into the other.[1] In the fully formed hair, they contain no remains of endoplasts. The medullary substance, like the cortical, proceeds from the metamorphosis of the indifferent tissue of the pulp, but the process, instead of being one of vacuolation and fibrillation, is essentially one of cellulation. The endoplasts, instead of elongating, remain rounded. Cavities are developed round them, whose partition walls become thick and granular. The cavities then gradually enlarging eventually open into one another, and the endoplasts disappear. The whole structure and mode of development of this tissue, in fact, show its complete identity with the "pith" of feathers, as we shall see more fully below.

The *hair sac* is an involution of the whole integument, and as such

[1] Griffith, Lond. Med. Gazette, 1848.

is composed of an enderonic and of an ecderonic portion. The former, which is continuous with the subcutaneous tissues, when well developed, consists externally of a network of fine elastic fibres, within which is a layer of homogeneous tissue containing endoplasts which are more or less elongated transversely, and which form the superficial layer of the enderon. Within this is a structureless layer, the commencement of the ecderon, enclosed by which are the representatives of the cellular ecderon, the so-called *rootsheaths*. These are commonly described as two, the *outer* (*a*) and the *inner* (*c*, *d*); the latter again being composed of two structures, an external, the *fenestrated inner rootsheath* of Henle, and an internal, which I described in 1845, and which may be called the *imperforate inner rootsheath*. The *outer rootsheath*, like the others, is thicker above than below, thinning out where it joins the bulb at the bottom of the sac. It consists entirely of tissue resembling that of the rete mucosum, and needs no particular description.

The *fenestrated inner rootsheath* lies in immediate contact with the outer rootsheath. It is composed of more or less rounded or polygonal flat plates, with faintly marked boundaries, united by their narrow ends, and leaving spaces between their sides (*fig.* 315. F). It is very tough and resistant, both to mechanical and chemical action, and no endoplasts can be seen in its elements. The *imperforate rootsheath* (*a*) is composed of flat thin flexible plates not unlike those of the preceding layer; but they present no intervals, their boundaries are strongly marked, and in the centre of each there is a peculiar, elongated, often more or less dumb-bell-shaped endoplast. In the human hair sac there are usually only one or two laminæ in this layer, but in Rodents there are said to be many.

If we examine a hair sac above the level of the bulb, it will be clear that these inner rootsheaths are not generated from the contiguous surface of the external rootsheath, as would at first seem probable. No transitional forms, in fact, are visible in the direction of the transverse diameter of the sac. Traced towards the base of the sac, however, it is obvious that opposite the lower portion of the bulb the inner layers of the outer rootsheath become metamorphosed into horny cells; and that of these cells, the inner are converted into the imperforate layer, while the outer undergo a more complete cornification, and lose all trace of their primitive endoplasts. The clefts which ultimately exist between these cornified plates are not present in the young state, but are the results of a secondary vacuolation. They have nothing to do with the disappearance of the endoplasts; for traces of the latter may be observed in the *centre* of horny plates, at

whose *edges* the clefts are commencing (*fig.* 315. F). It would appear, therefore, that the rootsheaths grow like the shaft of the hair itself not by addition to their surface, but by growth of their deep-seated inner ends.

Such is the composition of the growing hair; but the completely formed hair (see § 2. *Morphology*) presents very great differences in the minute structure of its inner termination. In the first place, the shaft runs out into an irregularly conical mass, like a worn-out painter's brush. It consists, at its extremity, entirely of cortical substance, and the cornification runs in irregular lines into the indifferent tissue, which occupies the bottom of the hair sac and represents both pulp and outer rootsheath. The inner rootsheaths terminate above this point, in an irregularly horny layer, which unites with, and is in a manner reflected into, the cuticle of the shaft, which ceases above its brush-like expansion. Finally, the outer rootsheath in the immediate neighbourhood of the inner, is metamorphosed into large horny cells, like those of the cellular ecderon. The development of these from the indifferent tissue of the outer rootsheath, may be very clearly traced. The periplast first becomes enlarged and marked off into definite granular areæ around each endoplast, and the limits of each area are metamorphosed into clear horny walls. The cavity which these inclose enlarges, and the endoplast, with its surrounding granular matter, remains attached to one wall, and then eventually disappears, while the cavities enlarge, and their walls thicken into clear horny "cells," which may eventually be detached from one another.

The whole process of the completion of the root of a hair, then, is simply a return of the diverticulum of the ecderon,—the metamorphosis of whose elements, so long as the hair was in course of formation, was guided and determined into distinct forms along certain fixed lines,—to its general tendency to undergo the ordinary cellular metamorphosis over its whole surface. With this return to its primitive tendencies, the increase of the hair of course ceases, and sooner or later it is pushed out and falls away.

The spines of the Porcupine, of the Hedgehog, and of the Echidna [1] present in their histological, as in their morphological relations, an interesting approximation to feathers. Externally, they are coated by a cuticle, while the principal mass of their walls consists, at the ends, of a fibrous horny substance; in the middle, there is added to this a medullary substance composed of polyhedral horny cells.

The section of the *shaft* of a fully-formed feather presents exactly

[1] See Bröcker (Reichert, Bericht. Müll. Archiv. 1849).

these constituents except the cuticle; the centre is occupied by *medullary substance* (*fig.* 317. B, *a*), composed of a coarsely granular horny substance excavated by polygonal cavities of about $\frac{1}{1000}$ inch in diameter, frequently if not invariably containing air, which adds to the dark hue (by transmitted light) arising from the granular opacity of the horny matter. At its edges, this tissue passes into the *cortical substance*, which, in a transverse section (*fig.* 317. D) appears as a clear homogeneous or slightly granular mass, dotted over by minute apertures, about $\frac{1}{10000}$ in. in diameter, and $\frac{1}{3000}$ in. apart. In a longitudinal section, on the other hand (*fig.* 317. C, *b*), the general mass appears obscurely striated in a longitudinal direction; and in the place of the circular apertures, we see elongated fissures, somewhat narrowed at each extremity, whose transverse sections constituted these apertures. The pointed ends of the fissures were continued by a line which could frequently be traced into some other fissure above or below, so that I conceive the fissures are in reality more or less complete canals.

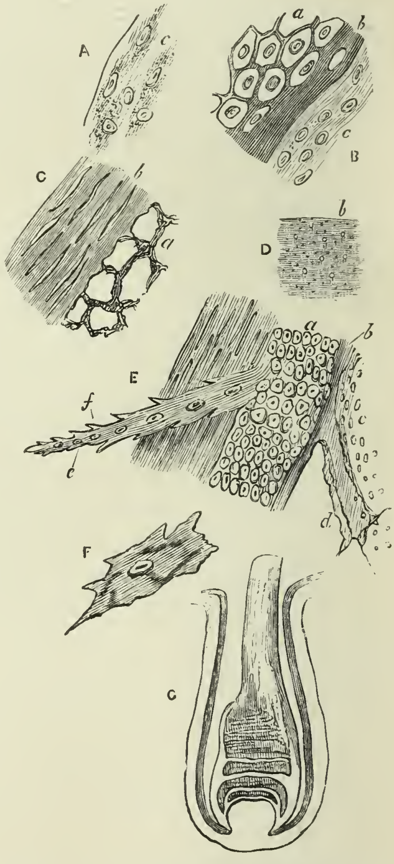


FIG. 317.—Feathers of the neck of the common Fowl. A, free edge of pulp; B, C, medulla and cortex; D, transverse section of cortex; E, a barb, with barbule partly detached from pulp; F, cornified cell, from rootsheath; G, horny diaphragms in the quill.

The *quill* of the feather is entirely composed of cortical substance; the *barbs* have the same structure as the shaft; the *barbules* present both cortical and medullary substances in a rudimentary condition. Each barbule in fact (*fig.* 317. E, *e*) exhibits along its axis a series of oval cavities, the remains of cells like those of the medulla, while its lateral portions are composed of striated horny matter like that of the cortex, and are produced into the curved and hooked lateral *processes* (*f*).

The polygonal cells of the medullary substance are produced from

the indifferent tissue of the pulp in exactly the same manner as those of an ordinary horny, cellular ecderon from that of the *rete mucosum* : that is to say, the periplast increases, and becomes marked out into polygonal areæ ; it then requires a horny consistence, and a stronger and stronger definition along the lines of demarcation, until polygonal "cells" (as in *fig.* 317. B, *a*) are formed. The walls of the latter now thicken and become granular ; the endoplasts disappear, and at length nothing is left but the honey-combed perfect medullary substance. The mode of formation of the *cortical substance* is the inverse of this. On examining the line of junction (*fig.* 317. B) of the pulp (*c*) with recently formed cortical substance (*b*), it is observable that the endoplasts do not become surrounded by cell cavities, but that the periplast acquires a granular, longitudinally fibrous, appearance ; while the endoplasts, though they are occasionally visible in the striated mass, soon completely disappear.[1] The elongated cavities or tubuli do not at first exist in the cortex, but are the result of a secondary vacuolation, and so far as I have been able to observe, have no relation with the pre-existing endoplasts. In fact, these canals, like those in the hair-shaft, the clefts in the fenestrated root-sheath, and the canaliculi of bone, must be regarded as the results of a secondary vacuolation. The feather sac resembles that of the hair in all essential points of structure except that the relations of the layers of the inner rootsheath are different. As in the hair, two layers may be distinguished in the inner rootsheath, an outer, strong, dark, horny membrane corresponding with the fenestrated membrane, and an inner delicate flexible layer, corresponding with the inner horny rootsheath. The former has a structure intermediate between that of the two layers of the inner rootsheath in the hair, consisting of irregular polygonal plates, which retain the remains of their endoplasts (*fig.* 317. F), as in the inner layer of the horny rootsheath, and do not become separated by fissures : while they resemble the plates of the outer horny rootsheath in their thickness, complete cornification and striated appearance.

The inner layer of the horny rootsheath is a delicate, often granular membrane, which closely invests the outer surface of the feather, and from presenting a cast of its elevations and depressions, has been called the outer "striated membrane" of the feather sac (*suprà*, § 2). It is a sheet of horny matter, in which traces of closely set endoplasts are discoverable. The inner (*fig.* 317. E, *d*) "striated membrane" is a membrane having a similar structure, possessing similar relations to the inner surface of the feather, and which is

[1] Compare Schwann, Untersuchungen, &c.

continuous with the so-called "pith" in the quill of a fully formed feather. The mode of development of these rootsheaths is identical with that of those in the hair, and therefore requires no further elucidation here.

Tegumentary glands.—The other conversionary productions of the ecderon which we have to consider, are the glandular appendages, which are always diverticula of the cellular ecderon inwards.[1] Under this head I include only those small glandular organs, which, so far as we know, have no reference to any other functions than that of cutaneous transpiration or fatty secretion, referring to the articles on special divisions of the animal kingdom for an account of those organs, such as the "water-vessels" of Echinoderms and Trematoda, the nidamental glands of Molluscs, the genital glands of Vertebrata and Insecta, which might strictly be regarded as productions of the integument.

Tegumentary glands in this limited sense are somewhat rare among the Invertebrata. They have, however, been observed in the Annelids, where they consist of delicate tubes, terminating internally by a blind extremity containing a single nucleated cell. Such glands exist on the ventral surface of the head and foot discs in Piscicola and are scattered all over the body in Clepsine and Nephelis. Similar glands are found opening upon the ventral surface of Argulus foliaceus,

Simple cœcal glands are scattered over the whole surface of the body of the Procession Caterpillars, opening at the points of the hairs; on the sides of the body in Myriapods, on the joints of the legs in Beetles and Bugs.

In Mollusca a peculiar, probably glandular, canal exists in the foot of certain Lamellibranchs, and glandular cœca have been observed in the lower surface of the foot in Paludina. A ciliated canal runs in the foot of Pulmonata, and receives glands on each side. The existence of cutaneous glands in the Cephalopods appears doubtful—at least, H. Müller could only find them as shell glands in the expanded arms of Argonauta.

Among the Vertebrata, Fishes, Ophidia, Chelonia and Birds, appear to possess no proper cutaneous glands[2]; in Sauria they attain

[1] Unless, indeed, these simple "mucous cells," described by Clark and Leydig in Fishes, and which are merely modified cells of the cellular ecderon, should be regarded as glands.

[2] Dr. Clark, in his excellent account of the skin of the eel (Trans. Mic. Soc. 1849), describes cutaneous glands in that animal. The so-called "glands" of the lateral line, however, have since been shown by Leydig to have a very different structure; and I confess I have not been able to convince myself of the existence of the other glands described by Dr. Clark. I can find nothing like them, except the strong perpendicular semi-elastic bands, which traverse and unite the bundles of connective tissue in this as in other fishes.

a very slight and local, but in Batrachia and Mammalia, an immense development. In the frog, the whole surface of the ecderon is beset with minute trifid apertures, so disposed between three epidermic cells, as to present a singular resemblance to the stomata of plants (*fig.* 318. B). These lead directly into spherical sacs (*fig.* 318. A. *d.*), which are lined by a continuation of the cellular ecderon, and lie in the superficial part of the enderon above its stratified layer (*fig.* 318. A. *g.*) (*vide infra*). Nerves (*f*) and vessels penetrate the latter to reach the superficial layer of the enderon, and ramify among these close-set glandular sacs. The sacs usually contain only a clear fluid[1]; they are contractile, and may be made to expel their contents by irritation of the nerves distributed to them.[2]

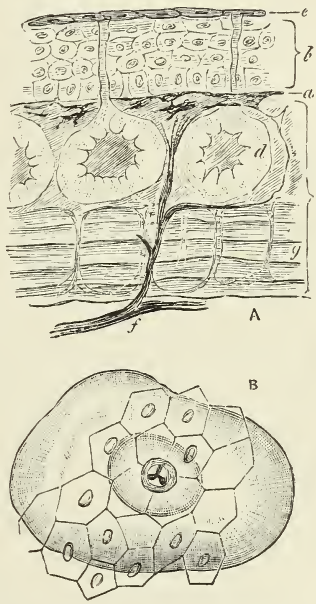


FIG. 318.—The cutaneous glands of the Frog. A, section ; B, superficial view.

In Mammals, we meet with two kinds of cutaneous glands, sebaceous and sudoriparous. The former are almost invariably developed in connection with the hair sacs, consisting in fact of diverticula of the Malpighian layer of the cellular ecderon of the upper portion of these sacs, whence their position is always superficial. The innermost cells of the solid process become filled with fat —break down, and pour their contents into the hair sac itself, by whose aperture they make their exit. Sometimes, as in the hairs of the head in man and in the pig's bristles, the sebaceous glands are very small and simple, while in other localities they throw out processes, and assume the appearance of complex racemose glands disposed like rosettes around the hair-sac, from which they are developed.

Sudoriparous glands.—These glands, like those just described, are, as Gurlt pointed out, simple, elongated processes of the deep layer of the ecderon, differing from the sebaceous glands chiefly in producing a clear fluid, instead of a fatty secretion. As Kölliker has shown, however, no line of demarcation is to be drawn on this ground, the

[1] Stated by Bergmann and Leuckart to have an irritating property in Triton.

[2] Ascherson : Haut-drüsen d. Frösche, Müller's Archiv. 1841. Czermak : Haut-nerven d. Frösche. Ibid. 1849.

secretion of the axillary sudoriparous glands in man being an essentially sebaceous substance. The sudoriparous glands are cylindrical cœcal tubes varying, in man, from $\frac{1}{100}$ to $\frac{1}{500}$ of an inch in diameter, whose walls are either thick or thin. In the former case they consist of a simple ecderonic cellular coat, contained within a prolonged sheath, formed by the uppermost layer of the enderon, and, like it, composed of a homogeneous or indistinctly fibrillated periplast, with imbedded endoplasts. Outside this, or rather forming part of it, is a layer of longitudinally-disposed smooth muscles, and the whole is coated, like the deep surface of the rest of the enderon, by a more or less distinct layer of connective tissue. In the thin-coated glands the muscular layer is absent, but the cellular ecderonic coat is frequently so thick that they possess no cavity at all. The thick-walled glands are met with in man in the axilla, scrotum, anal region, &c.; while those of the rest of the body are almost entirely of the thin-walled description. The glands terminate superiorly in undulating canals, which reach the surface of the enderon, and are continued to that of the ecderon by oblique channels excavated in its substance between its cells. Inferiorly, they form close coils, which lie in the subcutaneous areolar tissue, and receive twigs from the vessels in their neighbourhood.

In the other Mammalia, the general structure of the sudoriparous glands is as in man. In the sheep, according to Gurlt, they present the same coiled arrangement, while in the ox and dog they are straight and simple. In the ox they have rounded, dilated extremities, and are everywhere similar in shape and size. On the hairy parts of the body of the dog, they are small simple cœca, which are very difficult to discover; while on the ball of the foot of this animal they are very large and resemble those of man. Very large sudoriparous glands have likewise been observed upon the horse's prepuce.

Scales of fishes.—In the Ganoid fishes *Accipenser* and *Polypterus* the substance of the scales is composed of ordinary bone whose superficial layer is only denser than the rest, and exhibits a local development of fine branching tubuli; but in other fishes, two, if not three, distinct layers are usually distinguishable in the scales.

In many Plagiostomes, for instance, the placoid scales have the same composition as the teeth, consisting of a superficial layer of nearly structureless dense "enamel," or as Prof. Williamson more conveniently terms it, "Ganoin," while the deeper substance is composed of a tissue in every respect similar to dentine, whose innermost portion in some cases passes into true bone,—an addition which might be compared to that of the cement in the teeth. Leydig, indeed, has

shown that the resemblances between the scales and the teeth of Placoid fish extend even to their mode of development. If the pulp contained in the central cavity of the spine-like scale of a *Raia clavata* be pulled out, globular calcareous masses of $\frac{1}{1000}$ of an inch and upwards in diameter, and either solitary or adhering together in masses, will be found to be attached to its surface. "These globules are exactly analogous to the dentine globules described by Czermak, which in human teeth afford the formative material for the matrix of the dentine. What, however, appeared to me especially worthy of notice was the circumstance, that the most distinct and beautifully branched canals, having exactly the same appearance as those in the substance of the spine, were already visible in these isolated calcareous bodies, and on carefully examining the fine processes of the canals, no doubt could exist that they were only interspaces or gaps. On carefully adjusting the focus, in fact, it was obvious that one of these large calcareous globules is itself only an agglomeration of many smaller globules, and it could be observed that the gaps left between the latter became the fine processes of the tubules. From these facts, I believe that the correct mode of conceiving the growth of the substance of the spine is, to suppose that the calcareous matter is excreted from the vessels of the pulp, and then in all probability combined with organic matter, runs into smaller masses ; these unite together into larger ones, and become applied to the inner surface of the central cavity, coalescing, and thus adding to the thickness of the spine. Between the calcareous globules, however, canalicular gaps or tubules remain, which form a connected network and communicate with those branched cavities which already exist in the spine.

The scales of the Sharks and the dermal spines of the Rays, then, (and I would draw particular attention to this result,) are perfectly identical in structure with the teeth, even to the absence of nerves in the pulp, and must be united in the same structural group. I have already (On the Skin of Fresh-water Fishes, Zeitschrift für Wiss. Zool. B. iii. H. 4.) pointed out the close affinity between the scales of a number of osseous fishes and their teeth : and scales likewise present globules of calcareous matter, which become fused together to form the homogeneous substance of the scale. A process, corresponding with that which occurs at the surface of the pulp in the teeth and cutaneous spines, here takes place from the surface of the sac of the scale (Schuppentasche). The scales of osseous fishes, the spines of the Rays, and the scales of the Sharks, therefore, all belong to the series of dental structures, which in no respect interferes with the entrance of true bony tissue (like the "cement" in the higher animals)

into their composition, as we find to be the case in the scales of the Ganoids (Müller), and in the truly bony semi-canals which are attached to the scales of the lateral lines of many fishes."[1]

For the details of the various modes in which Ganoin, true osseous tissue, and those varieties of tubular, more or less dentine-like tissues, to which Prof. Williamson has given the names of "Lepidine and Kosmine," are combined together in the scales of Ganoid and Placoid fish, I must refer to that gentleman's memoirs, already so often cited.

In the Ctenoid and Cycloid fishes there is a superficial "Ganoin" layer composed of numerous thin structureless calcified laminæ, which are frequently thrown into folds, papillæ or spines. The deeper substance of the scale is composed of a series of layers of a membranous substance, each layer being composed of parallel fibres which take a different direction from those of the superficial and subsequent layers, so that the fibres of alternate layers cross diagonally. No endoplasts or cells are ever distinguishable among the fibres. In the deepest part of the scale these layers are entirely membranous: but in passing towards the surface, minute lenticular masses of calcareous matter make their appearance in the membranous substance. As Prof. Williamson justly states, these lenticular bodies are not developed between the membranous fibres and lamellæ, but in them: "they commence as a small calcareous atom, and increase in size by the external addition of new concentric laminæ; the direction of the latter not being parallel with, or having any reference to, that of the laminæ of fibrous membrane with which they so amalgamate; thus they are not depositions from, but growths in the membrane; which growths, as they increase in size, retain their primitive tendency to assume a lenticular form." Following the layers of the scale outwards, these isolated calcareous deposits not only enlarge, but ultimately become fused together, forming at length either a continuous calcareous mass in each layer, or presenting fissures which in some cases traverse the original lenticular calcareous deposits, in others are interstitial to them. I think one cannot but be struck with the complete analogy between the structure and mode of development here described and those which I have previously shown to obtain in the calcified tegumentary organs of the Mollusca and Crustacea. The ganoin layer corresponds very closely with the "epidermis" of the shell or test; the middle laminated calcified substance is formed by the fusion of concentrically laminated concretions deposited in a membranous matrix in the Fish, the Mollusk,

[1] Leydig: Rochen und Haie, 1852.

and the Crustacean alike ; while the deep uncalcified layers of the scale are represented by the "horny" laminæ which have escaped calcification in Haliotis or Unio, and still more closely by the fibrillated uncalcified layers of the Crustacean test.

Structure of the enderon.—The enderon of the Invertebrata is usually entirely composed of rudimentary connective tissue or of mere indifferent tissue, consisting, in the latter case, simply of a matrix with imbedded endoplasts, while in the former it is produced into plates and bands, never exhibiting, however, the peculiar bundles and elastic fibres which are met with in fully formed connective tissue.

In Paludina, according to Leydig, the pigment masses, which lie on the surface of the ecderon, are connected by "clear large cells, with a small parietal nucleus." From their occurrence, wherever in the higher animals connective tissue is found, Leydig calls them "Binde-substanz-zellen"—"Connective tissue cells ;" but, as he himself points out, they frequently contain carbonate of lime, and their relation is rather, like that of the similar cells in Piscicola, to fat.

A wonderful complication of structure is attained by the skin of the Cephalopoda. According to H. Müller,[1] who has recently made some careful investigations on this subject, there lie beneath the cellular ecderon in these animals : 1st, a fibrous layer, usually colourless, but occasionally white and glittering. 2nd, the layer with the chromatophora (*vide inf.*). 3rd, beneath these a peculiar layer, which gives rise to the colours produced by interference, the metallic lustre and intense whiteness of many localities. It consists frequently of regular plates, which evidently proceed from nucleated cells. 4th, deeper still lie the larger bundles of connective tissue, the muscles and the vessels.

In the Vertebrata, the superficial layer of the enderon is similarly composed of indifferent tissue, and of rudimentary connective tissue ; the former passing gradually into the latter, as we trace it inwards, developing its elastic element to a greater or less extent, and acquiring a more or less distinctly fascicular arrangement of its collagenous element. In the higher Vertebrata, these bundles are usually disposed as an irregularly felted mass ; but in Fishes and Batrachia, they form regularly superimposed horizontal strata, tied together by perpendicular columns, which penetrate the interspaces of the bundles, and spread out into the irregular connective tissue on the deep and superficial surfaces of the stratified mass (*fig.* 319. A). On the addition of acetic acid, it is seen that the boundaries of the strata are formed by

[1] Bericht, &c. Zeitschrift für Wiss. Zoologie. 1853.

irregular bands of elastic tissue, in which the remains of the primitive endoplasts may be seen (as in fibro-cartilage), whose strongest fibres are horizontal, though they send out others irregularly in all directions. The perpendicular columns are likewise composed of bundles of pale elastic fibres (*fig.* 319. B), and if the intersection of the horizontal with the vertical divisions be carefully examined, it is seen that the former are, as it were, given off by the latter, which thus gradually break up and thin out, terminating above and below in the elastic fibres of the unstratified superficial and deep layers. A horizontal section of this portion of the enderon presents a very peculiar appearance, the transparent vertical columns looking like radiating spaces, as which they were, in fact, at first described.

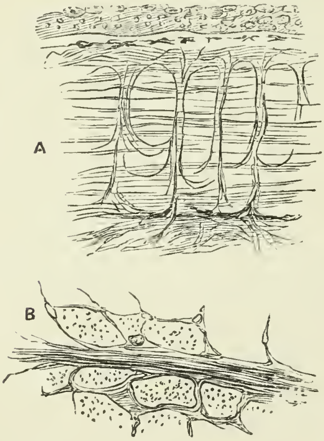


FIG. 319.—Enderon of the Skate.

Pigment of the enderon.—The enderon presents scattered masses of pigment, sometimes contained in cells and sometimes free, in many Invertebrata (Annelids, Trematoda, Echinoderms, Crustacea, Mollusca). In other Invertebrata and in the higher Vertebrata, the pigment is confined to the ecderon. In Fishes and Reptiles, however, a well-marked layer of pigment lies at the surface of the enderon in the form of scattered granules and of irregular more or less stellate masses which are not enclosed in cells. The silvery lustre of the skin of fishes is due to minute rods which constitute a layer at this surface, and should probably be regarded as a peculiar form of pigment granules.

In the Cephalopoda and some Gasteropoda among the Invertebrata, the integument undergoes during life the most extraordinary variations of colour, becoming overspread with successive clouds of the most vivid hues. These are produced by the contraction and expansion of peculiar sacs—the *chromatophora*—containing masses of pigment granules. According to H. Müller, (whose observations I have recently had the opportunity of repeating,) these are sacs attached to whose walls are contractile fibre cells arranged radially, and frequently anastomosing with those of other cells. They do not always contain pigment, but frequently present a distinct nucleus. Several layers of these chromatophora of different colours are frequently disposed, one over the other, in a given portion of the skin, and produce by their

different states of contraction, relatively to one another, successive changes in the colour of the spot.

Among the Vertebrata the Chamæleon, as is well known, presents similar phenomena.

Papillæ of the enderon.—The enderon is frequently produced into conical or cylindrical processes, which either merely contain a vascular loop, or are supplied, in addition, with special nerves. In the Invertebrata, we find, in the processes of the mantle into the shell of the Brachiopoda described by Dr. Carpenter, organs which, I have no doubt, must be regarded, like the corresponding processes in the Ascidians, as vascular papillæ. Among the Articulata like processes extend, in the Crustacea, through the whole thickness of the integument to its surface, giving rise to the colourless spots observable on the shell of the crab, for instance. I imagine, however, that these spots were usually occupied by a hair when the shell was thin. In the Mollusca, the marginal processes of the mantle of the Lamellibranchs and Gasteropods, the papillæ of Onchidium, &c. and those of Tremoctopus (H. Müller) are very probably both vascular and nervous papillæ like those of fishes.

Among the Vertebrata, fishes present large projecting papillæ, particularly about the region of the lips and operculum, which are both vascular and nervous. Simple papillæ (nervous?) are scattered over the surface of the body in Plagiostomes and some Ganoid fishes.

I am not aware that papillæ have hitherto been observed on the integument of Birds and Reptiles. In most Mammals, they are very small, if they exist at all, upon the general surface of the body, attaining a considerable size only in such organs as the ball of the foot (Cat, Dog), or on the muzzle. The Cetacea, however, appear to make a remarkable exception to this rule ; it is stated (Heusinger, Breschet, and Roussel de Vauzème) that the very thick integument of these animals is traversed by vascular and nervous papillæ, four or fives lines long, which extend as far as the outer horizontal horny layer of the ecderon, so that a horizontal section of the ecderon is like that of a horse's hoof. In man, again, the papillæ are, as is well known, so abundant as to have given rise to the term *pars papillaris*, for the superficial layer of the ecderon. The structure of those which appear to possess special nervous functions will be considered below.

Sensory appendages of the enderon.—Very little is known of the ultimate distribution of the nerves to the integument in the Invertebrata, but we are indebted to Leydig for showing that in certain Crustacea, Insecta, and Mollusca, it is very similar to what occurs in

the vertebrate classes. Thus in *Argulus foliaceus* the peripheral nerves become pale, and divide, and at the point of division there is a 'nucleus' as in the embryonic fibres of the frog. In *Artemia salina*, *Branchipus stagnalis*, and in the Heteropod Mollusk *Carinaria*, the termination of the tegumentary nerves is essentially similar. The larva of the Dipterous insect *Corethra*, presents even peculiar sensory appendages, in the delicate plumed hairs which beset the sides of the body. These are articulated in the ordinary way, and have an internal ligament, a sort of spring, attached to their base, which is enlarged and receives the enlarged and cellæform termination of a nervous twig. It will be obvious that this arrangement is peculiarly fitted for communicating the slightest vibration to the nerves.

In the Vertebrata (fishes, reptiles, man), the ordinary mode of termination of the integumentary nerves is in one or two plexuses, whence the fine terminal branches proceed, and end by dividing into minute branches indistinguishable from the imperfect elastic fibrils of the enderonic tissue. Loops have also been observed, but it is impossible to say whether, in any case, these are real terminations or not. Gerber and Kölliker have also described "nerve coils" in animals, and in the conjunctiva and lips of man.

The simplest form of sensory appendage in the Vertebrata is presented by the large papillæ of fishes, into which a bundle of nerve fibres enters, some of which terminate in the papillæ, while others, whose looped bands may be readily distinguished, probably pass out again.

In certain fresh-water fishes (Barbus, Leuciscus), Leydig has described papillæ of this kind, which have a cup-shaped depression at their extremities, lodging a globular mass of what he describes as modified epithelium.

Special modifications of the tissue of the papillæ for sensory purposes in the fingers, tongue, lips, &c. of man have lately been discovered by Meissner and Wagner, and described by them, under the denomination of the *Corpuscula tactûs*. Kölliker, who doubts their special relation to the tactile function, on the other hand, prefers to call these bodies, *axile corpuscles*. They are simply ovoid masses of imperfect connective tissue occupying the centre of the papillæ, and further distinguished by having their endoplasts and imperfect elastic fibrils arranged transversely to the axis of the papilla, so that they appear to be made up of transverse superimposed laminæ (*fig.* 320). One or two dark-contoured nerve tubules come up through the base of the papilla, and running along one side of the corpuscles, thin out and terminate, without, so far as I have been able to see, entering its substance.

In fact, these nerve tubules are, as Kölliker pointed out, accompanied by a delicate neurilemma and the axile corpuscle itself appears to me to be nothing more than the enlarged end of this neurilemma.

In Birds, a large proportion of the tegumentary nerves terminate in bodies which are, on the one hand, related to these axile corpuscles, and on the other to the well-known Pacinian bodies (*fig.* 322). They are, in fact, usually described under the latter name ; but their small size and superficial position, the paucity of their concentric lamellæ, and the transverse striation of the solid central axis, ally them closely with the corpuscula tactus. They are found in the skin around the sacs of the feathers, in the beak, and in the interosseus spaces of the forearm and leg.

FIG. 320.—A papilla with its Corpusculum tactûs surrounded by three vascular papillæ.

A special article (PACINIAN BODIES) has already been devoted to the organs of this kind which are met with in Mammalia, and it need only be added here, that late researches have shown that the Pacinian bodies of mammals, like those of birds, are solid masses of rudimentary connective tissue ; the appearance of capsules and of a central cavity, arising merely from the arrangement of the elastic element and the extreme transparency of the collagenous substance.[1] They are, in fact, nothing but thickened portions of the neurilemma, and the nerve which they enclose either passes through them, or more usually terminates, more or less abruptly, in the central solid axis.

In the article on the PACINIAN BODIES reference is made to the peculiar organs described by Savi in the Torpedines. These Savian bodies, in fact, are little more than Pacinian bodies converted into sacs by the development of a cavity between their central and peripheral portions. Now Leydig has discovered that these Savian bodies do not stand alone, but that they form a part of a great series of peculiar integumentary sensory organs, which are most characteristi-

[1] This fact was ascertained and stated independently and contemporaneously in 1853, by Leydig and myself. See Quarterly Journal of Micr. Science, No. V., and Siebold and Kölliker's Zeitschrift, B. v. Heft 1.

cally, if not solely, developed in the class of Fishes—the so-called *mucous canals* and *follicles*. It has long been noticed, in fact, that in osseous fishes one series of the scales along the sides of the body differ in their structure from the rest, giving rise to what is called the *lateral line;* and that a canal runs beneath these scales from the tail to the head on each side ; that then becoming connected with its fellow by a transverse branch over the occiput, each canal passes forward on the sides of the head, dividing into two principal branches, one of which following the course of the suborbital bones terminates at the end of the snout, while the other passes down on to the lower jaw. Similar organs, but having a more complicated arrangement, are known to exist in the cartilaginous fishes; but it is commonly supposed that these canals and follicles secrete the mucus with which the skins of fishes are lubricated. However, in a very beautiful series of researches, Leydig has shown that the mucus is furnished by the cellular ecderon, and that the so-called mucous canals and follicles are sensory organs. The limits of this article will not permit me to enter into any of the details of structure of these organs, but they may all be described generally as sacs or canals lined by a cellular investment, like that of the skin upon which they open, and filled with a more or less gelatinous substance. If the organ be a sac, a single protuberant knob, if a canal, a series of them project into the cavity. Each knob is covered by a coat consisting of tiers of much-elongated cylindrical cells. Its substance consists of more or less gelatinous connective tissue, and it receives a nerve (a branch of the fifth or of the vagus), whose fibres divide and become lost in its tissue. In the osseous fishes this nerve usually perforates the peculiarly modified scale of the lateral line, which supports and encloses the canal at these points. In the cartilaginous fishes the canals have sometimes special fibro-cartilaginous coats ; or if sacculi, a number of them may be contained in a common cartilaginous investment, as in the Chimæra. Leydig insists with great justice on the identity of the structure of these organs with that of the semicircular canals of the ear.

The connection of these sacs and canals with the corpuscula tactûs and Pacinian bodies appears to me to be clear ; for the knob which projects into the cavity of the mucous canal is homologous with the central " nucleus " of the Savian body, and this with the solid axis of the Pacinian body, and with the corpusculum tactûs, so that the " tactile " sac of the Chimæra, *e.g.*, may be said to be a tactile corpuscle which is connected with the surface of the integument.

No organ at all resembling these has certainly been met with,

above the class of Fishes, in either Reptilia or Birds, but in Mammalia there are structures which must, I think, be placed in the same category. About the lips and nose of almost all mammals in fact, there are certain long, strong hairs, the vibrissæ or "whiskers" (*fig.* 321). These in their general structure resemble ordinary hairs, but the sac of each, instead of lying free in the enderon, is enclosed in a second thick sac, composed of firm, dense, connective tissue, which attains at times an almost cartilaginous hardness. A looser areolated tissue connects this with the outer surface of the proper hair sac, and supports an abundant vascular network proceeding from vessels which enter at the deep end of the sac. Furthermore, a very considerable nerve pierces one side of the "sclerotic" coat near this end, and passes to the surface of the proper hair sac, upon which it spreads out and forms a nervous expansion, its fibrils dividing and subdividing, and so terminating.

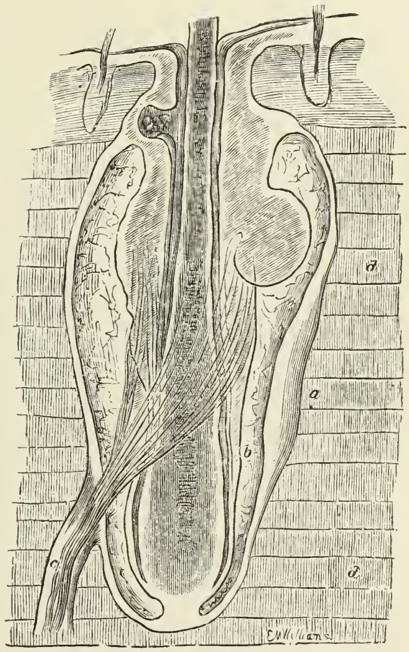


Fig. 321.—Vibrissa from the snout of the Mouse. *a*, "sclerotic" sac ; *b*, hair-sac ; *c*, nerve-trunk ; *d*, muscular fibres.

Considering the different habits of life of the mammal and the fish, I think one cannot but be struck with the similarity of plan between their vibrissæ and the "tactile" canals. The sensory impression is conveyed to the gelatinous contents of the canals in the fish by the vibration of the dense medium in which it lives ; while in the mammal the impulse is communicated by the contact of some external object with a long elastic hair lever ; but the final arrangement for the receipt and appreciation of the impressions is essentially the same in each case, nor indeed does it differ from that which is met with in the highest organs of sense.

Muscles of the enderon.—In the Invertebrata the great majority of the muscles are, as is well known, inserted into the integument, but those which are attached to the chromatophora of molluscs and to the spines of annelids and other worms, might be regarded as belonging more especially to the integumentary system.

In Fishes and Reptiles the superficial layer of striped muscles of the body is always more or less connected with the integument; but hitherto no unstriped fibres appear to have been detected in it. In Birds, however, the unstriped muscles attain a very great development, forming a thick layer whose bundles (*c*) run between and are attached to the sacs of the feathers (*fig.* 322).

In the majority of Mammals there is a special tegumentary striped muscle, which attains an enormous development in the hedgehog, while a mere rudiment of it remains in man, as the platysma myöides. Here, however, the striped "*peaucier*" muscle is replaced by the unstriped bundles which, as Kölliker has shown, run from the upper layer of the enderon to the bases of the hair sacs, and effect the various movements of which the hairs are capable.

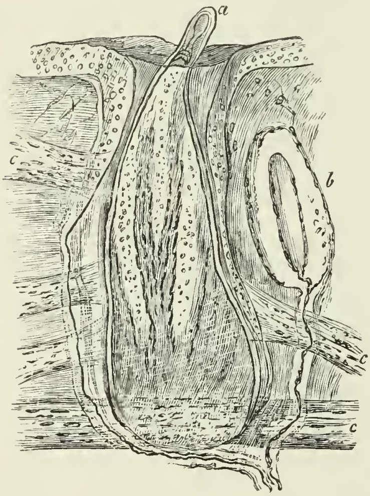


FIG. 322.—Pacinian body (*b*) and feather-sac (*a*) from the base of the mandible of a pigeon. *c*, muscles of the feather sacs.

Calcareous deposits in the enderon.—Deposits of this kind are very frequent in the Invertebrata. In the Pulmonate and some Gasteropod Molluscs, for instance, globular masses of carbonate of lime are scattered through the enderon, and would almost seem to take the place of fat. In nudibranchiate mollusks, such as the Doridæ, spicula of like nature are met with, and these sometimes unite into true internal shells, as in the genus Villiersia. The greater part of the skeleton of the Actinoid polypes, and the whole of that of the Ecinoderms, is composed of calcareous networks of this kind, and globular masses of calcareous matter are scattered through the enderon of the Tæniadæ, though the clear spherical bodies observed in these worms are by no means always of this nature. Whether these enderonic calcareous deposits ever take place in the Vertebrata appears to me to be, as I have said above, an open question, only to be decided by a very careful examination of the mode of growth of their so-called "dermal" bones.

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XXXIX

ON THE METHOD OF PALÆONTOLOGY.

Ann. Nat. Hist., vol. xviii., 1856, *pp.* 43-54.

THERE are two perfectly distinct aspects under which Living Beings may be studied—the Physiological and the Morphological. On the one hand, every living being exerts certain forces and performs certain acts or functions. It is the object of the physiologist to ascertain the precise mode in which these acts are performed, to refer them as far as possible to the ordinary laws of physics and chemistry, and when, as in many cases, the functions are highly complex, to analyse them into their elementary acts, and to determine by what part of the frame, by what special organs these are performed. With the form of these parts, with their connexion other than that which is involved in their coadjustment towards a common effect, the pure physiologist has no concern.

On the other hand, every living being has a definite form, and in all the higher living beings this form is complex; it is made up of a greater or smaller number of lesser parts, each of which has its own definite and appropriate figure. Now it is with these forms, with their mutual relations, with the laws which govern their association, that morphology is alone concerned. Although in practice the two branches of biological science are commonly more or less united, yet it would be quite possible to write a complete system of pure physiology without reference to morphology, and of morphology without reference to physiology. They are as distinct as in the mineral world are crystallography and chemistry. To put the case in another way. The different parts of every living being are all mutually related, they are subject to definite laws of correlation, but these laws of correlation are of two kinds essentially independent of

one another: there are physiological correlations and there are morphological correlations. Thus the teeth and the stomach are physiologically correlated, contributing as they do to the common end of alimentation; and inasmuch as this coadaptation towards a common end is the very essence of physiological correlation, the latter has sometimes received the name of *rational* correlation; for when the result to which a combination tends is obvious, we commonly imagine we can see the reason for that combination.

Since the validity of nine-tenths of the science of animal physiology involves the admission, that multitudes of the parts of animals are organs working towards a common end, I do not suppose that it ever has entered, or ever will enter, into the mind of any person conversant with the rudiments of that science to question the existence of physiological correlation between the different parts of animals. But how far that correlation is in any case to be called *necessary;* that is, how far in order to the due performance of a given function in any case it is impossible that the organs performing that function should be different from what we find them to be, is quite another question. Thus the teeth of a lion and the stomach of the animal are in such relation that the one is fitted to digest the food which the others can tear; they are physiologically correlated, but we have no reason for affirming this to be a necessary physiological correlation, in the sense that no other could equally fit its possessor for living on recent flesh. The number and form of the teeth might have been quite different from that which we know it to be, and the construction of the stomach might have been greatly altered, and yet the function of these organs might have been equally well performed. Nothing can be more uniform than the physiological ends which have to be attained by living beings; nothing more various than the modes in which they are attained; and it would, I think, in the face of these well-known facts, be the height of presumption to affirm that the function which we see in any case performed in a particular way could not possibly have been performed in any other mode.

If physiological correlations are however not *necessary;* if, so far as physiology is concerned, we have no right to say with Cuvier, that "Every organized being constitutes a whole, a single, and complete system, whose parts mutually correspond and concur by their reciprocal reaction to the same definite end. None of these parts can be changed without affecting the others, and consequently each taken separately indicates and gives all the rest;"—then a very important consequence follows, viz., that it is quite impossible to reason conclu-

sively on physiological grounds alone from any part of a living being to the whole.

I by no means assert that Cuvier, in enunciating the proposition quoted above, meant to exclude all but physiological considerations so completely as the words appear to indicate. On the contrary, his practice, no less than other passages of the remarkable essay from which that citation is taken, shows clearly that no man more fully understood the value of morphology. Nevertheless the words of the proposition are distinct enough to justify those who, guided more by authority than by right reason, have denominated it Cuvier's law of correlation, and, ambiguously supported by Cuvier's phraseology elsewhere, have imagined the principle which it involves to have been his guide in palæontological research.

A simple illustration or two, however, will show that the laws of physiological correlation alone are wholly incompetent to furnish such guidance. Suppose I find the jaw of a vertebrate animal with sharp cutting teeth imbedded in it, how far will physiology help me to determine the precise nature of the animal to which it belonged? The sharpness of the teeth may lead me to guess that they were used for cutting some soft substance. The shape of the articular condyle and that of the processes for muscular attachment may equally render probable the direction and force of its ordinary movements; but as to the rest of the organism, whether the teeth were for cutting up fish, flesh, fowl, or carrion, whether the creature itself was piscine or reptilian or mammalian,—on all these points no amount of mere physiological reasoning will help me. Nay, how do I know it is a vertebrate jaw at all; that it is a vertebrate bone and tooth substance? For anything physiology teaches me to the contrary, Invertebrate animals might develope osseous and dentinal tissue, and might possess appendages having the form of vertebrate jaws.

Every naturalist knows that Invertebrate animals do not thus mimic the Vertebrata, and he believes that they never have and never will do so; but his confidence is based, not on any physiological reasoning as to the impossibility of such a proceeding, but on his simple experience that it never does occur. He rests not on a deduction from the laws of physiological correlation, but on the morphological law that no Invertebrate animal ever possesses an organ having the form and structure displayed by the jaw in question. And this law is an empirical one; no further reason for it can be given than for the law of gravitation. The whole object of morphology is to ascertain *what* structural peculiarities invariably coexist with one another: *why* these structural peculiarities coexist is a question with which it does

not necessarily concern itself, and so far as the mere restorations of the palæontologist are concerned, it is a wholly irrelevant question. The empirical laws of morphology supply all that the palæontologist requires for this object.

Let us imagine that all existing animals had perished, but that their dead forms were gathered together and submitted to the investigation of some intelligent being from whom the knowledge that they had ever lived was concealed. He would of course remain entirely ignorant of physiology and all its laws. Life, if he were acquainted before only with physical and chemical phænomena, would be an inconceivability, and the conception of adaptation to purpose, of physiological correlation, would fail to suggest itself where nothing was known of actions or functions.

Nevertheless, by the careful comparison of one form with another, he would see that in one set of specimens certain structural peculiarities were invariably associated, in another set others, and he would thus arrive at precisely the same laws of morphological correlation,[1] and at the same classification of these dead forms as that which we have reached from our study of the living ones. He would not term Lions and Tigers and Wolves "Carnivora," for he would not even know that they eat anything, but he would assuredly form a group with pretty nearly the same limits as the Carnivora, simply because all these animals resemble one another, and differ from the rest in certain peculiarities of dentition, &c. So, again, he would group Oxen and Sheep and Deer together, because they present corresponding coexistences of structure, though, knowing nothing of their digestive processes, he would not call them "Ruminantia."

And now, after our imaginary being had made himself acquainted with the whole series of forms before him, and had established his great laws of morphological correlation and his classification, suppose that a mass of fragments of other creatures, more or less similar to those which he had first familiarized himself with, were placed before him, and he were desired to put these fragments together, and to reconstruct these dismembered forms, how would he proceed? Suppose the first bone which came to hand very closely resembled the jaw of a Deer, would he not naturally conclude—could he logically escape the conclusion—that in all probability the skull and limbs which belonged to this jaw were like those of a Deer also? And finally, supposing that, guided by this strong probability, he had selected a complete deer skeleton from the mass, all of whose parts

[1] Except so far as he would be deprived of the advantage of the study of development. This, however, obviously by no means interferes with the validity of the general argument.

were in such proportion to one another and to the jaw first discovered, as to accord perfectly with his already ascertained laws of correlation of form in the Deer species, could the validity of his restoration be questioned, because he knew nothing about the purposes of all these parts or their physiological correlation?

What additional certainty would he gain by now learning that the Deer had once lived—that it was herbivorous—that its teeth and internal organs were all exquisitely adjusted to its mode of life? He would say, That is all very beautiful, and I am very glad to know it; but such considerations did not in the least help me to pick out the bones which belonged to the jaw, nor do they add a grain of certainty to that which I already feel as to the justice of my restoration. Indeed, my method tells me a great deal that yours is quite silent about. I knew empirically that the kind of tooth and jaw placed before me was always associated with horns, with slender limbs, and with cleft hooves; but I could never have divined these things from knowing that the jaw and tooth were specially adapted to a herbivorous diet.

Surely all this is so obvious as to need no great amount of demonstration, and no less clear is its application to the question, What is the method of palæontology? How is it that we are able to restore an extinct animal from some fragments of its skeleton? It is by deduction from those empirical laws of morphology which express the invariable coexistences of structures, so far as observation has yet made them known to us, and it is by this method only. When once the general nature of an extinct animal has been ascertained, the laws of physiology may help us to very useful hints and guesses; but the fundamental step towards the determination of the nature of any unknown fragment, whether recent or fossil, are purely morphological, and, so far as they are concerned, physiology might be non-existent.

The truth of what has just been asserted must long have been familiar to every thinking botanical palæontologist; and I have never met with any indication, either in their works or in conversation, that the botanists imagined they were guided in their determinations of extinct plants by any reference to physiological correlation, or by any other method than deduction from purely empirical morphological laws. Nor does the palæontologist, who concerns himself with invertebrate forms, often seek for help from physiology. In fact, the total absence of any acquaintance with physiology which many excellent palæontologists manifest, is a curious illustration of the justice of my line of argument, as it nowise interferes with the

soundness of their work,—so long as they confine themselves to such purely morphological questions as are involved in the restoration of extinct forms.

Nor can I find that *in practice* those palæontologists who have studied the Vertebrata trouble themselves much about physiological correlations or adaptations to purpose. The reader of Cuvier's "Ossemens fossiles" might begin at the tenth volume and read on to the second, and while he would be astounded at the enormous knowledge of the laws of morphology—of the observed coexistence of parts which it displays—he would find himself very rarely troubled with any remarks upon physiological correlations or adaptations; and any which might offer themselves would be entirely subordinate to the great object of the work, which is, to apply the purely empirical laws of morphological correlation, which have been ascertained to obtain among living beings, to the elucidation of fossil remains.

It is with no little surprise, therefore, that in the first volume he finds, or seems to find, the principle of physiological correlation brought prominently forward, in the celebrated 'Discours sur les Révolutions,' as *the* guide in palæontology, as the especial means by which the determination of mammalian fossils, at any rate, is effected. I say, *seems* to find; for, after all, if the master's words be studied carefully, it will be discovered that his followers are more Cuvierian than Cuvier.

In fact, as I have already particularly pointed out, in a lecture which I recently delivered before the members of the Royal Institution, Cuvier gives up the principle of physiological correlation, both explicitly in words and implicitly in practice, as an exclusive guide in palæontological research; and he expressly admits the necessity of a reference to the laws of morphological correlation.

But while admitting the importance of both methods, the physiological and the morphological, he gives to the former by his words a prominence which it by no means has in his practice; or perhaps I may more justly say, that his phraseology is ambiguous, from his having confounded the two methods together, under the one term of "principe de la corrélation des formes dans les êtres organisés." Those who will read carefully from p. 178 to p. 189 (ed. 4, 1834) of the 'Discours,' will find that this confusion exists throughout. Thus, if we take one of the opening passages already cited (p. 178):—

"Every organized being constitutes a whole, a single, and complete system, whose parts mutually correspond and concur by their reciprocal reaction to the same definite end. None of these parts can

be changed without affecting the others; and, consequently, each taken separately indicates and gives all the rest."

The first paragraph here embodies the principles of both physiological and morphological correlation. The second paragraph, however, regards physiological correlation only, and the statement which it contains is not true. We have no evidence to justify us in asserting that no one part can be changed without affecting all the others. On the contrary, we have abundant evidence to show that allied species, for instance, differ in only a single character; which would be an impossibility if a change in one part sensibly affected all the rest.

Cuvier then goes on to show, in a very beautiful manner, the physiological correlation which exists between the parts of a Carnivore, concluding with the well-known phrase, "in the same way the claw, the scapula, the condyle, the femur, and all the other bones taken separately, will give the tooth, or one another; and by commencing with any one, he who had a rational conception of the laws of the organic œconomy could reconstruct the whole animal."

If Cuvier means by "the laws of the organic œconomy," (and the context would indicate that he does,) its physiological laws merely, then I must venture to say, that I believe this assertion to be incorrect. I do not believe that the problem—given a tooth or a bone, the mode of life of an animal, and the laws of physiology, to find the structure of other parts of the body of that animal,—is a soluble one.

In fact, Cuvier himself, in the very next paragraph (p. 182), almost gives up his own principle. I give his own words:—

"Ce principe est assez évident en lui-même dans cette acceptation générale pour n'avoir pas besoin d'une plus ample démonstration; *mais quand il s'agit de l'appliquer, il est un grand nombre de cas où notre connaissance théorique des rapports des formes ne suffirait point si elle n'était appuyée sur l'observation.*"

And again, in concluding, at p. 187 Cuvier says:—

"Et, en adoptant ainsi *la méthode de l'observation comme un moyen supplémentaire quand la théorie nous abandonne*, on arrive à des détails faits pour étonner. La moindre facette d'os, la moindre apophyse, ont un caractère déterminé relatif à la classe, à l'ordre, au genre et à l'espèce auxquels elles appartiennent, au point que toutes les fois que l'on a seulement une extrémité d'os bien conservée on peut avec de l'application, et en s'aidant avec un peu d'adresse de l'analogie et de la comparaison effective, determiner toutes ces choses aussi sûrement que si l'on possédait l'animal entier."

Finally, at page 184, after speaking of those invariably coexistent

peculiarities of organization among the Ruminants, which have no apparent physiological connexion, Cuvier says :—

"Cependant puisque ces rapports sont constans il faut bien qu'ils aient une cause suffisante ; mais comme nous ne la connaissons pas, nous devons supplier au défaut de la théorie par le moyen de l'observation ; elle nous sert a établir des lois empiriques qui deviennent presque aussi certaines que les lois rationelles, quand elles reposent sur des observations assez répetées : en sorte qu'aujourdhui quelqu'un qui voit seulement la piste d'un pied fourchu, peut en conclure que l'animal qui a laissé cette empreinte ruminait, et cette conclusion est tout aussi certaine qu'aucune autre en physique ou en morale."

I confess that, considering the Pig has a cloven foot, and does not ruminate, the last assertion appears to me to be a little strong. But my object is not to criticise Cuvier, but simply to show that nothing could be more marked than his appreciation of the value of the merely empirical laws of morphology, as applied to palæontology, nothing more erroneous than the popular notion, too much favoured by his own language, that his method essentially consisted in reasoning from supposed physiological necessities. In the lecture above referred to, I not only maintained this view, but I further asserted, and endeavoured to prove, that not only are popular and other writers thus mistaken in interpreting Cuvier, but that Cuvier himself was in error in ascribing to the laws of physiological correlation that primary importance in palæontology which he undoubtedly does give them. I brought forward, in fact, the doctrine which I have argued at greater length in the preceding pages, viz. that palæontology, so far as it consists in the restoration of extinct forms, is entirely based upon deductions from the empirical laws of morphology; that its conclusions, so far, would be as valid if the whole science of physiology were non-extant, and if we knew nothing of final causes or adaptations to purposes.

The publication of the abstract of the lecture has elicited a brusque attack from Dr. Falconer, which, coming as it did from the pen of a palæontologist of high repute, caused me at first, I must confess, no slight alarm ; the more so as Dr. Falconer, in his laudable desire at once to extinguish heresy, had, I found, taken the somewhat unusual course of widely circulating his little pamphlet.

The perusal of Dr. Falconer's essay, however, soon relieved me from my only real source of uneasiness, by demonstrating very clearly that Dr. Falconer had been far too much in a hurry either to master the real question in dispute, to read what I had written with atten-

tion, or to quote me with common accuracy and fairness. In fact, I have not the good fortune to be among the "*tantis* viris" de quibus "modeste tamen et circumspecto judicio pronuntiandum est," and it is clearly in Dr. Falconer's opinion not worth while to use much circumspection in dealing with the opinions of mere ordinary "viri."

The first evidence of Dr. Falconer's entire misconception of the point at issue meets one in the title-page—"On Prof. Huxley's attempted refutation of Cuvier's Laws of Correlation in the reconstruction of extinct Vertebrate Forms." It is repeated at page 477. "Nearly three-fourths of Mr. Huxley's abstract are devoted to the first head, viz., Natural History, regarded as knowledge, the leading feature of which is an attempt to refute the principle propounded by Cuvier, that the laws of correlation which preside over the organization of animals, guided him in his reconstruction of extinct Forms." Nothing can be more entirely incorrect than the assertion contained in the latter part of this paragraph. I did *not* attempt to refute any one of Cuvier's laws of correlation. There is not a passage in my lecture which can be justly so interpreted. I merely endeavoured to prove, and I can find nothing in Dr. Falconer's essay to show that I did not prove, first, that the *physiological* laws of correlation which Cuvier laid down are not as universally and necessarily applicable as he seems to have imagined; secondly, that his physiological laws of correlation are of wholly subordinate importance in palæontology, if not absolutely unimportant, the really important laws by which he worked being those morphological laws, those empirical laws of coexistence which, as I have said, no man lays down more clearly, but to which he nevertheless ascribes in words, though not in practice, a subordinate place. This entire misunderstanding of the real point under discussion vitiates the whole of Dr. Falconer's paper. It is again repeated at p. 481, just after Dr. Falconer has gravely warned us how necessary are "precision of thought and expression in disquisitions of this kind."

So again, at p. 487, Dr. Falconer says:—

"The argument drawn by Mr. Huxley from instances of empirical relation in the vegetable kingdom *against* there being necessary or reciprocal relation in the high classes of the animal kingdom is exactly of this character."

I assert that no one who carefully reads my abstract will find the slightest ground for the assertion that I have ever made use of any such argument as that imputed to me by Dr. Falconer. What I say in regard to plants is:—

"And if we turn to the botanist and inquire how he restores fossil

plants from their fragments, he will say at once that he knows nothing of physiological necessities and correlations."

To any unprejudiced reader of ordinary intelligence it will be quite obvious that the question of the existence of physiological correlation between the parts of plants is here utterly untouched. The question is whether the physiological or the morphological laws of correlation guide the botanical palæontologist. I affirm the latter, and I am supported by every botanist with whom I have spoken on the subject.

Dr. Falconer writes at p. 487 :—

"Nature has formed living beings upon certain types which constitute the basis of methodical nomenclature, and the correlation of part to part and organ to organ is adjusted in subordination to these types."

Now what is this but an admission of all that I have contended for, namely, that the physiological correlation of organs is wholly subordinate to their morphological or, in other words, typical correlation? What is it that Dr. Falconer attacks, after all? And this question becomes all the more bewildering, when we find at p. 480 :—

"Our first remark is, where and by whom has the principle of the 'utilitarian adaptation to purpose' been used as an instrument of research? Mr. Huxley avers that its value as such has been enormously overrated. If so, by whom has it been ever used? From the prevalence of adaptations and mechanisms in nature suited to the production of certain ends we reason up to the agency of an all-wise, powerful and benevolent Designer. But the inference is a product not an *instrument* of the research, and to call it the latter is simply a misuse of terms."

Surely Dr. Falconer can understand that adaptation to purpose is adaptation to use, and that therefore adaptation to purpose may well be said to be 'utilitarian.'

In answer to the next part of his inquiry, I must refer him to Dr. Whewell;[1] and with regard to the last part, the misuse of words is Dr. Falconer's. I am not speaking of any inference from the principle, but of the principle itself.

But the most curious proof that Dr. Falconer has not taken the trouble to read with attention or think over carefully the statements contained in my abstract is yielded by the passage at p. 480, begin-

[1] Philosophy of the Inductive Sciences, vol. ii. pp. 87, 88; and again, p. 78 :—"This idea of a final cause is an essential condition in order to the pursuing our researches respecting organized bodies."

ning, "Mr. Huxley contrasts the two as opposite dogmas." Dr Falconer here takes two parts of the same argument, thrusts them into opposition, and is then excessively puzzled to discover that he can find no "opposition or incompatibility" between them. However glad I may be to have Dr. Falconer's testimony to the connexion of the two parts of my argument, even *malgré lui*, I think he would have done well to have read the passage twice before entangling himself in it.

Dr. Falconer writes at p. 490 :—

"This invariable coincidence may be, as has been shown above, either *empirical* or *necessary*. Çuvier, like a true interpreter of nature, employed both indifferently in his restorations, accordingly as they were presented to him, and professed it. This important fact is *nowhere* recognized by Mr. Huxley, who argues the case throughout as if Cuvier had excluded the empirical and admitted only of necessary correlations."

This is in the teeth of the passage of my abstract, which Dr. Falconer himself quotes at p. 487 : "And if it were necessary to appeal to any authority save facts and reason, our first witness would be Cuvier himself, who in a very remarkable passage, two or three pages further on ('Discours,' pp. 184, 185), implicitly surrenders his own principle." Surely this amount of careless incorrectness is hardly venial. Surely I may quote to Dr. Falconer his own courteous words, "rarely in the history of science has confident assertion been put forward in so grave a case upon a more erroneous and unsubstantial foundation."

Just after reproaching me at p. 482, as I conceive unjustifiably, with affirming a case to be one of Cuvier's selection, which is not so, Dr. Falconer falls into the precise error which he wrongfully attributes to me.

"Let us now take the case as put by Mr. Huxley, and suppose that the Brown and White Bears were only met with in the fossil state ; but with the proviso of the other living species being known to us as at present."

What I say is, "If Bears were only known to us in the fossil state." Dr. Falconer's proviso, in fact, is the precise nullification of my argument, and yet he still ventures to quote it as mine. So again at p. 483, after discussing the Bear question, Dr. Falconer states, "Mr. Huxley next takes in hand the opposite case of the *Ungulate Herbivora*, as put by Cuvier." Dr. Falconer's assertion is inaccurate ; I do *not* next take in hand the *Ungulate Herbivora* ; any one who will read my abstract may see that the discussion as to the Bears comes

at the end of the argument about the Ungulata, forming not a separate question or opposite case, but part of the same.

But here as elsewhere, Dr. Falconer seems to forget the important distinction between a question of detail and one of principle. If physiological arguments are good at all in the way Cuvier put them, they must be universal in their application, in which case any exception is fatal; on the other hand, if they be of limited application, before we can apply them in palæontology, we must first have ascertained to what group the subject of our studies belongs by other means, and these can only be the application of morphological laws.

I trust I have now brought forward sufficient evidence to justify my accusation of misrepresentation and misconception on Dr. Falconer's part, and I would most willingly leave the subject, were it not necessary in defence of myself and others to advert to one or two other points in Dr. Falconer's attack. In two of these, accuracy as to matters of fact is involved. The first relates to the Stonesfield Mammal, a title which has been applied as much to the Phascolotherium as to the Amphitherium. Dr. Falconer asserts, that I have been unhappy in my citation of this case, because the Amphitherium is an Insectivore, and because the Phascolotherium has fewer teeth than the Amphitherium. Candour might have led Dr. Falconer to quote a little more of Prof. Owen's opinion as to the latter animal than he does.[1] If he had combined careful thought with candour, he would have perceived that inasmuch as the Phascolotherium possesses forty-eight teeth (four more than the typical number in Mammals), and *has* the strongly inflexed angular process, it precisely fulfils the conditions of my argument. In point of fact, however, the number of teeth is an irrelevant consideration. The other question of fact relates to the structure of the Sloth's tooth; when Cuvier speaks of the alternation of substance in the teeth of an Ungulate animal, he obviously refers to that peculiar alternation of vertical plates of enamel, dentine and cement, which the teeth of the typical Ungulates present. A difference of structure in layers parallel to the crown of the tooth, is of course possessed by every Carnivore, and it is this kind of arrangement which the Sloth also presents. I venture to think, therefore, that this objection to my argument is like most of Dr. Falconer's, and to use his own words, "more specious than valid."

[1] See British Fossil Mammals, pp. 55 and 56. Professor Owen especially warns us against concluding "too absolutely" that the Amphitherium "may not have combined the more essential points of the Marsupial organization" with the slighter inflection of the angle of the jaw.

I have left untouched many points in Dr. Falconer's essay, not because they cannot be answered, but because I conceive they will answer themselves. Under this category I leave such passages as those at p. 488, the singular bad taste of which will cause Dr. Falconer, in his cooler moments, far more annoyance than they have occasioned to any one else, except his friends. But I cannot pass without more grave comment, the allusion, at p. 477, to the audience which I had the honour to address. Dr. Falconer's apparent ignorance of the nature of the Friday evening audience at the Royal Institution—one which the best men in this country approach gravely and earnestly, knowing as they do that, whatever be the "mixture" of their hearers, there is pretty sure to be among them a fair jury of their peers,—can be his sole excuse for the tone of his remarks.

XL

OBSERVATIONS ON THE STRUCTURE AND AFFINITIES OF HIMANTOPTERUS.

Quart. Journ. of the Geol. Soc., vol. xii., 1856, *pp.* 34–37.

FROM what has been stated in the preceding pages, it would appear that the following propositions embody all that is at present certainly known with regard to the great structural features of the genus *Himantopterus.*

1. The body is composed of a comparatively small carapace, succeeded by eleven or twelve free segments, the last of which is bilobed, lanceolate, or wide anteriorly and acuminated posteriorly.

2. At the margin of the carapace on each side lies a rounded or oval eminence, which there is every reason to regard as an eye.

3. The free segments have no appendages. The cephalothorax presents three pairs: an anterior, probably chelate pair, occupying the position of antennæ; a middle pair of broad, short, foliaceous, serrated organs, which have the appearance of mandibles; a posterior pair of long flattened, jointed appendages, terminated by an oval palette, and not improbably having an articulated filamentous appendage attached to their penultimate or ante-penultimate joint.

4. Lastly, many parts of the body of *Himantopterus* present a peculiar imbricated sculpture, resembling that exhibited by *Pterygotus.*

Assuming these data to be correct, the question is,—In what group of animals can we find an analogous structure? and there are obvious reasons for at once narrowing the field of inquiry to the *Crustacea*, and confining the search to the different subdivisions of that great group.

Analogies, if not for *Himantopterus*, at least for the very closely allied genus *Eurypterus*, have been sought by different naturalists among the *Pœcilopoda*, the *Phyllopoda* (particularly *Apus*), and the

Copepoda; and M. Milne-Edwards has suggested that *Eurypterus* possibly holds an intermediate position between the *Copepoda* and the *Isopoda*.

1. If we compare *Himantopterus* with *Apus* we find points of resemblance in the form and position of the sessile eyes,—in the position of the antennæ and of the great natatorial feet, and, to a certain extent, in their form,—in the structure of the jaws,—and finally, if *Apus productus* be compared with *Himantopterus acuminatus* and *H. bilobus*, in the terminal segment.

The discrepancies, however, are even more striking and important. The number of free segments in *Apus* is thrice as great as in *Himantopterus*; the carapace extends as a free fold far back over them; all the thoracic, and the great majority of the abdominal segments possess foliaceous appendages (which would certainly have been preserved in as perfect a state as other similarly constituted parts, had they existed in *Himantopterus*); and lastly, the penultimate segment carries long articulated styliform appendages.

2. A certain similarity between *Himantopterus* and *Limulus* in their carapace and eyes, the large size of the terminal segment and the chelate form of the antennæ in both, may be regarded as the most salient resemblances of the two genera. To these might be added a sculpture, not altogether unlike that of *Himantopterus*, on some parts of *Limulus*, and a certain resemblance in fundamental structure between the last ambulatory feet of *Limulus* and the great swimming members of *Himantopterus*.

The differences consist in the number and great development of the locomotive members in *Limulus*, the coalescence of its abdominal segments, their well-developed appendages, and the much smaller total number of segments.

3. *Himantopterus* resembles many Copepods in the form and relative proportions of the carapace and free segments, in the sessile position of the eyes, in the great locomotive antennæ and post-buccal appendages, and in the absence of the majority of the abdominal appendages.

But the thoracic appendages are always well developed in the Copepods, and the number of free segments is never so great as in *Himantopterus*.

While the relations of *Himantopterus* with the Pœcilopods, Copepods, and Phyllopods, then, must by no means be overlooked, they would appear not to be sufficiently close, while the differences, on the other hand, are too numerous to justify its arrangement in either of these families.

There is another Crustacean group, however, which presents a much greater approximation to *Himantopterus* in some of its forms,—the family of the Stomapods.

This small and not very well-defined group occupies nearly a central position among the *Crustacea*; and its members, like those of most central groups, while presenting a strong general similarity, differ very widely in details. The genus usually regarded as the type of the family—*Squilla*—is not more like *Himantopterus* than an ordinary Macruran would be; but if we turn from *Squilla* to *Ericthys* and *Mysis*, and thence to *Cuma* and its allies, we shall find we have passed by a series of insensible gradations from the close ally of the Podophthalmous *Macrura* to a sessile-eyed Crustacean, with the internal antennæ almost rudimentary, with a very small carapace, like that of a Copepod in its proportions, and with twelve free segments, the anterior of which only carry appendages, all the abdominal ones, except the penultimate, being in some cases deprived of them.

The characters just mentioned are common to the genera *Cuma*, *Bodotria*, *Alauna*, and *Calyptoceros* (the last a new genus lately discovered by myself in the Bristol Channel): and, in addition, *Calyptoceros* (and probably *Cuma*) exhibits very markedly that peculiar sculpture which forms so prominent a feature of *Himantopterus.*

The differences between these " Cumoid " crustaceans and the latter genus consist principally in the shape of the antennæ and the development of the thoracic appendages in the former, each thoracic segment being provided with a pair of simply constructed members. In addition there is a pair of appendages to the penultimate abdominal segment, of which no trace has been found in *Himantopterus.*

As regards the two former discrepancies, however, we find in *Ericthys* that the three posterior pairs of thoracic appendages are reduced to mere rudiments, even the two pairs which precede them being very small. The largest of all the thoracic appendages are the first and second maxillipedes, the former being terminated by an oval plate-like joint. The external antennæ carry a similar oval plate on a long stem.

Reductions and modifications of the appendages of a Cumoid Crustacean of a similar character to these would produce a form wonderfully similar to *Himantopterus.*

But such reductions and modifications carried still further, and bringing us still nearer the ancient form, are to be met with, not, indeed, in any adult Crustacean at present known, but in those remarkable larvæ of the Podophthalmous *Malacostraca* which were once known under the name of *Zoœa.*

In their earliest condition these larva possess sessile eyes, a short carapace, a long jointed abdomen without appendages, and with the terminal segment sometimes entire, sometimes bifid ; the only appendages beside the minute trophi, consisting of a single pair of antennæ and a varying number of maxillipedes, so modified in form, as to serve, in conjunction with the abdomen, as a powerful swimming apparatus.

The nearest approach to *Himantopterus* which could be constructed out of the elements afforded by existing Crustacea, then, would be produced by superinducing upon the general form of a Cumoid Crustacean such a modification of the appendages as we find among the Zoææform Macruran larvæ.

It must not be supposed, however, that, because on this account *Himantopterus* may with some propriety be termed a "*larval*" form it is therefore an "*embryonic*" form, or represents any *embryonic* stage of Crustacean development. On the contrary, so far as it is "*larval*" so far it is not "*embryonic*," inasmuch as the form of the Decapod larva is a wide and sudden deviation from the regular course of embryonic development in the Crustaceans in apparent adaptation to peculiar exigencies.

Nothing has produced more confusion in the application of natural history to geological problems than the ambiguous use of the word "embryonic," applied as it is, sometimes in the sense of "correspondence with a developmental stage," sometimes in that of "similarity to a larval condition." The structure of *Himantopterus* is anything but embryonic in the former, proper sense,—very much so in the latter.

XLI

FURTHER OBSERVATIONS ON THE STRUCTURE OF APPENDICULARIA FLABELLUM (Chamisso).

Quart. Journ. Microsc. Sci., vol. iv., 1856, *pp.* 181–191.

In a paper read before the Royal Society in 1851, I gave an account of a very singular animal which had been frequently observed and described under various names, as *Appendicularia* (Chamisso), *Oikopleura* (Mertens), *Fritillaria* (Quoy and Gaimard), *Vexillaria* (J. Müller), and *Eurycercus* (Busch), but whose precise place in the animal kingdom was still a matter of doubt. The essential points in that account will be found in the following extracts :—[1]

* * * * *

"The animal has an ovoid or flask-like body one-sixth to one-fourth of an inch in length, to which is attached a long curved lanceolate appendage or tail, by whose powerful vibratory motions it is rapidly propelled through the water."

"The smaller extremity of the animal is perforated by a wide aperture (*d*) which leads into a chamber, which occupies the greater part of the body, and at the bottom of this chamber is the mouth. The chamber answers to the respiratory cavity of the *Tunicata*, and is lined by an inner tunic distinct from the outer ; the space between these, as in the *Salpæ*, being occupied by the sinus system.

"On the side to which the caudal appendage is attached, an endostyle (*c*), altogether similar to that of the *Salpæ*, lies between the inner and outer tunics ; and opposite to this, or on the ventral side close to the respiratory aperture, there is a nervous ganglion, to which is attached a very distinct spherical auditory sac, containing a single, also spherical, otolithe. The sac is about 1-200th of an inch in diameter. The otolithe about 1-800th, figs. 1, 2, 4 *a*.

[1] Nova Acta Acad. Curiosorum, t. xi. pars secunda, pp. 313 and 314.

" Anteriorly, a nerve is given off from the ganglion (*a*) which becomes lost about the parietes of the respiratory aperture; another large trunk passes backwards (*b*) over the left side of the œsophagus, and between the lobes of the stomach, until it reaches the appendage, along the axis of which it runs, giving off filaments in its course, fig. 2."

" There is no proper branchia; but that organ seems to be represented by a richly-ciliated band or fold (*e*) of the inner tunic, which extends from the opening of the mouth forwards, along the ventral surface of the respiratory cavity, to nearly as far as the ganglion; when it divides into two branches, one of which passes up on each side, so as to encircle the cavity (*f*). This circlet evidently represents the 'ciliated band' of *Salpa.*

" The mouth (*g*) is wide, and situated at the posterior part of the ventral parietes of the respiratory chamber. The œsophagus (*h*) short, and slightly curved, opens into a wide stomach (*i*) curved transversely, so as to present two lobes posteriorly.

" Between the two lobes, posteriorly, the intestine (*k*) commences, and passing upwards (or forwards) terminates on the dorsal surface just in front of the insertion of the caudal appendage (*l*).

" The heart lies behind, between the lobes of the stomach. I saw no corpuscles, and the incessant jerking motion of the attached end of the caudal appendage rendered it very difficult to make quite sure even of the heart's existence."

" The caudal appendage (A) is attached or rather inserted into the body on the dorsal surface just behind the anus. It consists of a long, apparently structureless, transparent, central axis (*m*), rounded at the attached, and pointed at the free end. This axis is enveloped in a layer (*o*) of longitudinal, striped, muscular fibres; which form the chief substance, in addition to a layer of polygonal epithelium cells, of the broad alary expansion on each side of the axis."

" The only unequivocal generative organ I found in *Appendicularia* was a testis (*p*), consisting of a mass of cells developed behind and below the stomach, enlarging so much in full-grown specimens as to press this completely out of place.

" In young specimens the testis is greenish, and contains nothing but small pale circular cells; but in adults it assumes a deep orange-red colour, caused by the presence of multitudes of spermatozoa, whose development from the circular cells may be readily traced.

" This orange-red mass, or rather masses, for there are two in juxtaposition, is described by MERTENS as the 'Samen-behälter' or vesiculæ seminales. He describes them as making their exit, bodily,

from the animal, and then becoming diffused in the surrounding water. This circumstance, indeed, appears to have furnished his principal reason for believing these bodies to be what the name indicates.

"The spermatozoa have elongated and pointed heads about 1-500th of an inch in length, and excessively long and delicate filiform tails.

"MERTENS describes as an ovary, two granulous masses, which he says lie close to the vesiculæ seminales, and have two ducts, which unite and open into this 'ovisac.'

"This appears to me to be nothing more than the granulous greenish mass of cells and undeveloped spermatozoa, which exists in the testis at the same time as the orange-red mass of fully-developed spermatozoa.

"I saw nothing of any ducts, nor do I know what the 'ovisac' can be, unless it be a further development of an organ which I found in two specimens (fig. 3 *q*), consisting of two oval finely-granulous masses, about 1-300th of an inch in diameter, attached, one on each side of the middle line, to the dorsal parietes of the respiratory cavity, and projecting freely into it.

"Still less am I able to give any explanation of the extraordinary envelope or 'House' to which, according to MERTENS,[1] each *Appendicularia* is attached in its normal condition. I have seen many hundred specimens of this animal, and have never observed any trace of this structure; and I have had them in vessels for some hours, but this organ has never been developed, although MERTENS assures us that it is frequently re-formed, after being lost, in half an hour.

"At the same time it is quite impossible to imagine, that an account so elaborate and detailed, can be otherwise than fundamentally true, and therefore, as MERTENS' paper is not very accessible, I will add his account of the matter, trusting that further researches may clear up the point.

"The formation of the envelope or 'Haus' commences by the development of a lamina from the 'semicylindrical organ' (ganglion?). This, as it grows, protrudes through the opening at the apex of the animal (respiratory aperture). Its corners then become bent backwards and inwards, and thus a sort of horn is formed on each side, the small end of which is turned towards the apex of the animal, while its mouth looks backwards, downwards, and outwards.

[1] I have given this passage at length in order that others may be led to seek its explanation. Leuckart and Gegenbaur have been as unsuccessful as myself in finding any such structure; but that it should be purely imaginary seems past belief.

"At the same time two other horns are developed upwards (the animal is supposed to have its small end downwards), one on each side. These are smaller and more convoluted than the others.

"This four-horned structure consists of a very regular network of vessels, in which, at the time of the development of the organ, a very evident circulation is visible; the blood-corpuscles streaming from the attached end of the organ. 'The clearness with which the circulation was perceptible, together with the great abundance of vessels and the large extent over which they were spread, were circumstances which led me (says MERTENS) to believe this truly enigmatical structure to be an organ, whose function was the decarbonization of the blood. The ease with which the animal becomes separated from this organ is no objection to this view; the necessity there seems to exist for the reproduction of the latter rather confirming my opinion.'

"It is highly desirable that more information should be gained about this extraordinary respiratory organ, which, if it exist, will not only be quite *sui generis* in its class, but in all animated nature. And in a physiological point of view, the development of a vascular network, many times larger than the animal from which it proceeds, in the course of half an hour, will be a fact equally unique and startling.

"For my own part, I think there can be no doubt that the animal is one of the *Tunicata*. The whole organization of the creature, its wide respiratory sac, its nervous system, its endostyle, all lead to this view.

"In two circumstances, however, it differs widely from *Tunicata* hitherto known. The first of them is, that there is only one aperture, the respiratory, the anus opening on the dorsum; and secondly that there is a long caudal appendage.

"As to the first difference, it may be observed, that, in the genus *Pelonaia*,[1] an undoubted Ascidian, there are indeed two apertures, but there is no separation into respiratory and cloacal chambers. Suppose that in *Pelonaia* the cloacal aperture ceased to exist, and that the rectum, instead of bending down to the ventral side of the animal, continued in its first direction and opened externally, we should have such an arrangement as exists in *Appendicularia*.

"With regard to the second difference, I would remark, that it is

[1] I would particularly remark that the statement that there is no separation between the branchial and cloacal chambers in *Pelonaia* is erroneous. At the time this paper was written I had not examined *Pelonaia* (whose structure, as I have since found, differs in no essential point from that of an ordinary *Cynthia*), and I must have misunderstood the verbal information given by my lamented friend Professor E. Forbes.

just the existence of this caudal appendage which makes this form so exceedingly interesting.

"It has been long known that all the Ascidians commence their existence as larvæ, swimming freely by the aid of a long caudate appendage; and as in all great natural groups some forms are found which typify, in their adult condition, the larval state of the higher forms of the group, so does *Appendicularia* typify, in its adult form, the larval state of the Ascidians.

"*Appendicularia*, then, may be considered to be the lowest form of the *Tunicata*; connected, on the one hand, with the *Salpæ*, and on the other with *Pelonaia*, it forms another member of the hypothetical group so remarkably and prophetically indicated by Mr. MacLeay, and serves to complete the circle of the *Tunicata*."

In 1854 Dr. Rudolph Leuckart published, among many other valuable contributions to zoological science, a memoir on *Appendicularia* (for a copy of which I am indebted to the courtesy of the Author.)[1]

In several points Dr. Leuckart's view of *Appendicularia* differs from my own.

1. With regard to the "oval finely-granulous masses" attached on each side of the dorsal parietes, Leuckart states that they are by me considered to be "probably the ovaries." My words, it will be observed, hardly justify this assertion; I merely stated that they seem to be a further development of what Mertens *calls the ovisac*, which is a very different proposition. Dr. Leuckart's own view of these bodies, "that they are the earliest indications of the subsequently-formed stigmata," p. 84, is one with which I am, like Gegenbaur, unable to agree. In fact, as will subsequently appear, Dr. Leuckart has overlooked the true branchial apertures, unless indeed what he describes as the anus be one of them. The anal aperture, he states, is "situated on the right side, near the middle line, and exhibits a strong ciliary movement." Now, the anus is really in the middle line, and the ciliary movement which it exhibits could hardly be thus characterized, but, as will be seen below, the description would perfectly apply to one of the branchial apertures.

2. Dr. Leuckart failed to discover spermatozoa in the organ which is described by me as a testis. Nevertheless, it will be shown by-and-by that there can be no doubt that such is its real nature.

3. Finally, Dr. Leuckart arrives at the conclusion that *Appen-*

[1] Zoologische Untersuchungen von Dr. Rudolf Leuckart, Heft. II. Salpen und Verwandte.

dicularia is a larval form, and not, as I had suggested, an adult animal.

In 1855 Dr. Carl Gegenbaur, a very careful and excellent observer, published a memoir[1] on *Appendicularia*, containing the results of more extensive investigations than had hitherto been made. Adopting the view that *Appendicularia* is an adult form, Dr. Gegenbaur constitutes four species of the genus, *A. furcata*, *A. acrocerca*, *A. cophocerca*, and *A. cærulescens*. The most important and novel point in Dr. Gegenbaur's paper, however, is the discovery and description of the true branchial apertures, which had been overlooked by all previous observers, Dr. Leuckart and myself included. Dr. Gegenbaur says (l. c., p. 415)—

"If now we return to the branchial sac, the most remarkable objects are the two respiratory clefts which lie on its ventral wall and partially embrace the entrance into the œsophagus. Hitherto, none of those who have investigated the *Appendicularię* have recognised the true import of these organs, although Mertens saw them in *Oikopleura Chamissonis*, and Busch (in *Eurycerus pallidus*) would, in all probability, have understood them had he only borne in mind the typical structure of the Ascidians. Neither Huxley nor Leuckart have mentioned these respiratory apertures."

After describing the apertures, Gegenbaur proceeds—

"Exact observation shows that they are not simple apertures in the branchial sac like those of the Ascidians, connecting its cavity with the surrounding space; but that each is prolonged into a short tube which converges more or less towards its fellow on the ventral face."

In *A. furcata* these two tubes run

"At first parallel with one another downwards (if the animal be supposed to have its anterior part directed upwards, as in the figures), then form a knee-like curve inwards, running directly towards one another, and then entirely vanish, so that nothing more could be made out as to their mode of termination. The function of the respiratory apertures is therefore, in this case, entirely different from that which they perform in the Ascidians, in which the water passes through the branchial clefts, and, after aërating the blood contained in the network of the branchial vessels, collects in the space between the mantle and the branchial sac, to be eventually poured out of the cloacal aperture; while in our *Appendicularię* the water is led back

[1] Bemerkungen ueber die organization des Appendicularen, Siebold und Kölliker's Zeitsch, B.VI.

by tubular prolongations of the branchial clefts into the body, so as either to become directly mixed with the blood, or by some further ramifications of the tubes to act through their thin walls on the surrounding blood. Which of these possibilities really occurs must remain, for the present, undecided; for although in *A. cophocerca* the end of the respiratory tube may be seen very clearly, yet it is still uncertain whether a bent prolongation of it may not be continued from this point, and may not, by presenting a transverse sectional view, give rise to the appearance of an end. I will enter no further in this place into the discussion of possibilities, my principal object being the statement of facts. However, I believe I have demonstrated that there is a tolerably-marked difference between the respiratory system of the Ascidians and that of the *Appendicularię*, expressed morphologically by the tube proceeding from the respiratory apertures of the latter."

Excessively puzzled to understand how structures so well marked and so obvious as these should have escaped my notice, I was, as may be imagined, very desirous to re-examine *Appendicularia*; but although its occurrence in the British Isles was already recorded,[1] I hardly hoped to find it at accessible distances from the shore. During a few calm days last autumn, however, the water of the Bristol Channel, near Tenby, in Caermarthenshire, swarmed with *Appendicularię* (in company with annelide and crustacean larvæ, *Sagitta*, echinoderm larvæ, *Medusę*, and *Noctilucę*), very little different from the southern species which I had previously described, and I gladly seized the opportunity of repeating my observations.

The length of the body of different specimens varied very much; from one-fifth of an inch to a fifth or sixth that size. The caudal appendage was three or four times as long as the body, broad, flattened, and rounded at its extremity. The whole animal was usually colourless, except that the stomach had a brownish hue. In one instance, however, the caudal appendage was stained of a bright crimson colour, from what cause I know not.

With regard to the internal anatomy of the animal, I have, in the main, to confirm the statements I originally made. The oral aperture appeared to be more distinctly bilabiate than I had observed it to be in the southern species, the upper lip hanging over the aperture, and being, as it were, enclosed by the concave edge of the lower. The test forms a thick coat upon all parts of the body, except the posterior region, over the testis, where it is excessively thin. It often separates

[1] On the coast of Scotland. See Forbes and Hanley, "British Mollusca," vol. iv. p. 247.

from the outer tunic in a very curious manner, becoming thrown into folds and sacculations ; and I was almost inclined to seek here for Mertens' "Haus," had not his account been so circumstantially different.

The distance between the walls of the pharynx and the outer tunic appeared to be considerably greater than in previously-observed specimens, on the neural side, so that the blood-sinuses were here very large, becoming still wider near the ganglion, in consequence of the outer tunic being raised at this point into a transversely-convex protuberance, gradually diminishing towards the sides of the body. The pharynx is richly ciliated, and narrows posteriorly, its wall nearly following the contour of the stomach, so that it assumes the shape of a cornucopia, its tapering hinder portion bending up to terminate in the right division of the stomach. With regard to the endostyle, I have nothing important to add to my previous account, except that I believe it to be here, as in other Ascidians, the optical expression of the thickened bottom of a fold or groove of the branchial sac. The large apertures described by Gegenbaur (*c*), at once strike the eye, not only from their size, but from the vehement action of the long cilia with which they are provided. I can in no way account for having overlooked them, and I see nothing for it but to accept the fact of the omission as a practical lesson in scientific charity. The pharynx passes on each side into a funnel-like prolongation (*b*, *c*), with its apex directed towards one side of the rectum. The dilated base of this prolongation is continuous with the pharynx, its comparatively narrow apex *opens externally* beside the rectum. In the mid-length of this conical canal is a thickened circular band (*d*), formed towards the pharynx of a series of cellæform bodies, placed in a single series, end to end, and externally to this of a transversely-banded substance. It is from this latter portion that the cilia take their origin. They are arranged in several tiers, are very long, and have a strong wavy motion.

That we have here a direct communication between the pharynx and the exterior, and not, as Gegenbaur states, a communication between the pharynx and certain internal canals, was made clear to me, not only by direct observation of the external apertures, but by feeding the animals with indigo. In two specimens this experiment succeeded perfectly ; but it was very curious, that while in the one the current set *in* at the mouth and *out* at the apertures, in the other the current was in precisely the opposite direction, *in* at the apertures and *out* at the mouth. The wide stomach is bent backwards upon itself, so that its two halves or lobes are pretty nearly parallel, leaving,

however, an interval in which the heart is situated. The right lobe is quadrate in outline, and undivided, but the left is irregular and lobulated. The inner surface of the stomach is papillose and ciliated, and many yellowish granules are scattered through the substance of its walls. The intestine arises from the upper angle of its left lobe, bends to the right, and then, when it reaches the middle line, passes forward to the anal aperture. The rectum is ciliated, and, as before, I was unable to find any trace of the tubular "hepatic" system, so general among the other Ascidians.

The heart (*o*) is large, and occupies a transverse position between the two lobes of the stomach, laterally, being more closely in contact with the right lobe, and the testis and base of the caudal appendage, antero-posteriorly. I was unable to observe any blood corpuscles, nor could I discover any sign of that reversal of the direction of the contractions so general among the other Ascidians. The absence of corpuscles would have rendered it almost impossible, under ordinary circumstances, to discover the direction of the circulating currents, but in one individual, the testis, having attained its full development, had broken up within the body, and the sinuses were filled with dark masses of spermatozoa. The heart, in full action, propelled these in a regular course up one side of the caudal appendage and down on the other (Müller has already described such a current in his '*Vexillaria*'), forwards on the hæmal side, and backwards to the heart on the neural side. This individual was particularly instructive also, by affording corroborative evidence as to the nature of the pharyngeal canals. Had these been in any way connected with the sinus system, as Gegenbaur supposes, the spermatozoa could hardly have failed to pass into them. Nothing of the sort occurred however; they passed round in the sinus between the walls of these canals and the outer tunic without the slightest extravasation, and their dark hue gave the contour of the canals only a better definition than it had before.

The testis was always present; small, discoid, and apparently attached by minute radiating filaments to the parietes in the younger specimens, it assumed the bilobed form in the larger ones, occupying a large space behind the alimentary canal. Individuals with fully-developed spermatozoa were comparatively rare. In that just referred to, the spermatozoa had rod-like heads, about 1-7000th of an inch long, with very long, delicate, and filiform tails; and the testis was reduced to a mere transverse band, the greater part of its substance having apparently been shed in the form of spermatozoa. Of a vas deferens I could find no trace.

The rounded bodies (*m*) on each side of the branchial cavity

anteriorly, appeared sometimes to present an internal clear cavity, and might then be easily mistaken for ova. But the absence of any germinal spot, the uniformity in appearance of their bodies, in all individuals hitherto examined, and their position, are very great objections in the way of any such view of the matter.

I must confess that the evidence adduced by Gegenbaur appears to me insufficient to prove that the bodies which he describes in other *Appendiculariæ* as ovaria are such organs, and for the present I think it is safest to conclude that the female organs of *Appendicularia* are unknown.

With regard to the nervous system and the organs of sense, the only additional observations of importance refer in the first place to the caudal nerve, upon which I found at regular intervals small ganglion-like enlargements (Pl. X. [XXVIII.], fig. 4), from which, as well as in their intervals, minute filaments were given off to the adjacent parts. The largest of these ganglia is the lowest, and when the appendage and the body are parallel, it is about opposite the end of the rectum. The nerve here receives a coat of minute rounded corpuscles, so that an oval mass, about 1-300th of an inch long, is formed, from whence numerous minute fibrils radiate. The other ganglia contain not more than two to five such corpuscles.

Gegenbaur states that if *Appendicularia furcata* be examined from the dorsal surface, an S-shaped cleft, ciliated at its edges, will be observed to the right of the ganglion. The cleft, which occurs only in this species, pierces the wall of the branchial cavity, and puts it in communication with the sinus system.

Seeking for this "cleft" in my *Appendicularia* (*flabellum—cophocerca ?*), I came upon a slightly different, but I have no doubt, corresponding organ. This is a pyriform sac (*q*), about 1-800th of an inch in length, presenting at its wider end an aperture with a produced lip, communicating with the branchial cavity, and by its narrower extremity abutting upon the ganglion. The sac was richly ciliated within, and I have no doubt whatever that it is the homologue of that "ciliated sac," whose existence under different forms appears to be universal among the Ascidians. There is every reason, however, to regard this as an organ of sense, and it never communicates with the sinus-system, so that probably Gegenbaur's statement may be regarded as an error of interpretation.

I could discover no transverse muscles in the caudal appendage, but only an upper and a lower layer of longitudinal fibres, between which the axis of the tail was enclosed. Whether this central axis is a solid body, or a membranous capsule filled with fluid, I cannot say,

but it is assuredly closed at both ends. Its closed and rounded proximal extremity is readily seen, and I feel confident that there is no such communication between the heart and the interior of the axis as Gegenbaur supposes. In the individual already referred to, in which the spermatozoa were effused into the general current of the blood, none entered the axis of the caudal appendage.

The discovery of the external openings of the pharyngeal canal and of the true nature of the supposed "ciliated cleft," appears to me to possess peculiar interest, in that it eliminates those structural peculiarities hitherto supposed to exist in *Appendicularia*, which were in discordance with the general plan of the Ascidians. That an Ascidian should have apertures in its pharynx, establishing a communication between its cavity and the sinus system, would be a great anomaly; but that *Appendicularia*, being an Ascidian, should possess a ciliated sac, and that the wall of its pharynx should possess ciliated apertures or stigmata, establishing a communication between its cavity and the exterior, independent of the mouth, is only a strengthening of the evidence of its truly Ascidian nature.

Again, while the existence of these apertures establishes further most interesting relations of *representation* between *Appendicularia* and the larvæ of Ascidians, especially of *Phallusia*, it cuts away all ground for any supposed relations of *affinity* between the two. In *Phallusia*, it is true, as Krohn has shown, the cloaca is at first double, and each half, which might be regarded as the equivalent of the outer half of the pharyngeal canal in *Appendicularia*, opens by an independent aperture; but then the anus, instead of opening externally, terminates in one of these cavities. The enormous size, coarse ciliation and very small number of the pharyngeal stigmata in *Appendicularia*, too, are wholly unlike anything larval.

The development of the nervous system and of the organs of sense is quite opposed to the supposition that *Appendicularia* is a larval form; and, in answer to Leuckart's suggestion that developed spermatozoa and ova are found in insect larvæ, I would urge that, in these matters, it is hardly safe to judge of one class by analogical arguments drawn from another. I am not aware that such early development of the reproductive products has ever been observed in any mollusk.

The discovery of the true branchial apertures in *Appendicularia* appears to me to bear no less importantly upon the moot question of the homologie of the Tunicata and Polyzoa, by removing all doubt as to the truly pharyngeal nature of the branchial sac in the Ascidians. But, if it be a pharynx, it cannot be the homologue of the conjoined

tentacles of the Polyzoa, which are entirely pre-pharyngeal structures.

Whatever may be the result of future inquiries as to the arrangement of the female organs in *Appendicularia*, I cannot doubt that in *A. flabellum* we have an adult form in a male state. Whether the female has a totally distinct form, or whether the ova are developed in the same form at a subsequent period (I have observed individuals so young that it is hardly conceivable that the ova should be developed at an earlier period), is a problem of very great interest, but for whose solution I see no materials at present. Considering the abundance in which *Appendicularia* occurs on our own shores, the collection of the requisite data ought to present no great difficulties to those who possess leisure and the opportunities of a sea-side residence; and to any such person, whose eye may fall upon these pages, I commend the investigation as one which will amply reward him.

EXPLANATION OF PLATE X. [XXVIII.]

Fig. 1. *Appendicularia flagellum*, seen from the side to which the caudal appendage is attached, *i.e.*, the dorsal or hæmal side.

Fig. 2. Body of *Appendicularia*, magnified, side view.

Fig. 3. Body of *Appendicularia*, magnified, dorsal view.

Fig. 4. Caudal appendage; showing the great nerve, with its ganglionic enlargements.

A. Body. *B.* Appendage.

a. Oral aperture.

b. Pharynx, giving off its lateral canals.

c. External opening of these canals.

d. Ciliated circular bands, corresponding with the stigmata of the branchial sac in ordinary Ascidians; but here forming part of the wall of the canal *b*, *c*.

e. Anus.

f. Rectum.

g. Œsophageal narrowing of the pharynx.

h. Right lobe of stomach.

i. Left lobe.

k. Testis.

l. Axis of caudal appendage.

m. Rounded granular masses projecting from the hæmal wall of the pharynx, and of doubtful nature.

n. Endostyle; here, as elsewhere in Ascidians, the optical expression of the thickened bottom of a groove or fold, continuous at its edges with the epipharyngeal bands.

o. One end of the heart.

p. Ganglion.

q. Ciliated sac.

r. Stolithic sac.

s. Nerve trunk.

t. Ganglionic enlargements upon its caudal portion.

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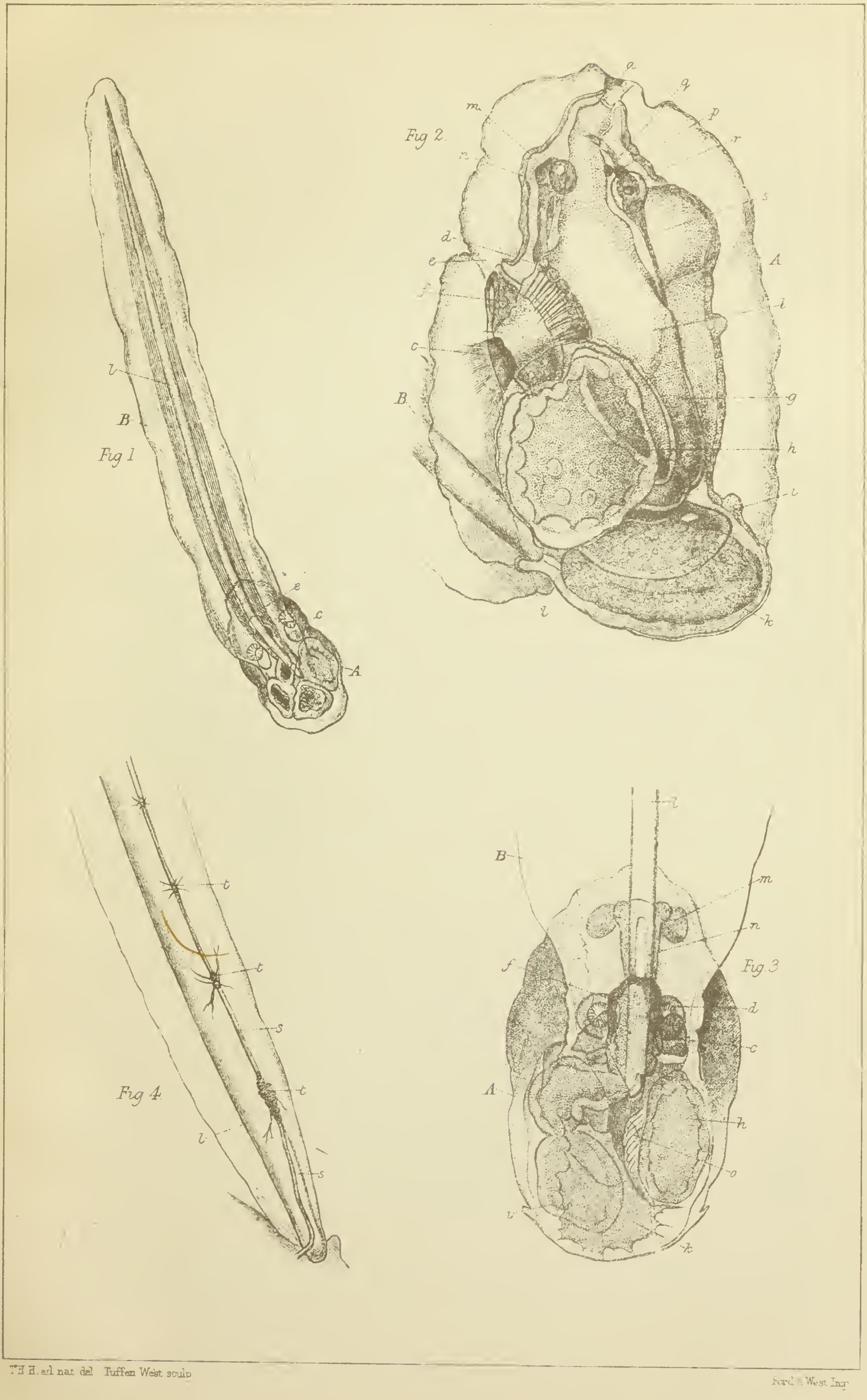

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XLII

NOTE ON THE REPRODUCTIVE ORGANS OF THE CHEILOSTOME POLYZOA.

Quart. Journ. Microsc. Sci., vol. iv., 1856, *pp.* 191–192.

OBVIOUS as are the ovicells and partially-developed ova of the *cheilostome Polyzoa*, the precise position of their ovaria and testis has not yet been determined ; the general idea that the ova are developed within the ovicells being wholly an assumption. The investigation of the question is not without difficulty, on account of the delicacy of the ova in their young condition, the greater or less opacity of the ectocyst, and the obstruction offered by the other viscera if the cells be viewed in any of the positions which they ordinarily assume, lying, that is, on their front or back faces. By tearing up a polyzoarium, with needles, into single series of cells, and causing one of these series to lie upon its side, I found the process of examination much facilitated.

In the younger cells of *Bugula avicularis*, I find that, as in many of the hippocrepian Polyzoa, there is a cord, or funiculus, connecting the extremity of the stomach with the bottom of the cell, and attached to this I found, close to the stomach, a single small pale ovum, commonly possessing a double germinal spot. At its lower attachment, on the other hand, the funiculus is surrounded by a mass of minute, pale, spherical corpuscles. In these cells, no ovicells were as yet developed ; but in older cells they make their appearance as diverticula of the ectocyst and endocyst, having their internal cavity continuous by a narrow neck with that of the cell. A valvular aperture eventually becomes developed at the lower part of their anterior face.

In such older cells, the ovicell is at first empty, and we find the ovum attached to the funiculus increasing in size, and acquiring a

reddish coloration ; but in those still further advanced, a similar, but larger and redder, body makes its appearance in the ovicell, and after undergoing yelk-division becomes a ciliated embryo. In these older cells, again, we find the granular mass at the bottom of the cell gradually developing into a mass of spermatozoa, which eventually float loose in the cavity of the cell.

I have no doubt, therefore, that in *Bugula avicularis* the ovarium is situated at the top of the funiculus, the testis at its base ; that impregnation takes place in the cavity of the cell, and that the ovum passes from thence into the ovicell—there, as in a marsupial pouch, to undergo its further development. The testis has a similar form and structure, and its position is invariably at the bottom of the cell in *Bugula flabellata*, *B. plumosa*, and *Scrupocellaria scruposa*, but that of the ovarium varies greatly. Thus in *B. flabellata* the ovarium is placed at the middle of the back of the cell, and is not directly connected with the funiculus ; in *B. plumosa*, it lies at the apex of the back of the cell ; in *Scrupocellaria scruposa*, it is at the upper and back part of the cell. The ovarium rarely presents more than one or two ova.

XLIII

DESCRIPTION OF A NEW CRUSTACEAN (PYGOCEPHALUS COOPERI, HUXLEY) FROM THE COAL-MEASURES.

Quart. Journ. of the Geol. Soc., vol. xiii., 1857, *pp.* 363–369.

PLATE [XXIX.].

THE following account of a very remarkable new Crustacean has been drawn up from the examination of three specimens, two of which are the property of R. S. Cooper, Esq., of Bilston, while the third belongs to the Manchester Museum. The last-mentioned is the most perfect, and may therefore be conveniently described first, as No. 1 (Pl. XIII. [XXIX.], fig. 1).

It was obtained from the coal-shales at Medlock Park Bridge, and consists of an ironstone-nodule split into two pieces, a larger and a smaller. The face of the latter exhibits a relief of the fossil, while the opposed surface of the larger piece presents the corresponding cast. Exclusive of the appendages, what we may call the body of the fossil (fig. 1 *a*) measures about $1\frac{1}{3}$ inch in length, and has a width of rather more than $\frac{5}{8}$ths of an inch at its widest part.

The one end of the body (fig. 1 *b*, *c*) is much broader than the other, and has the form of a semicircular disk, the base of the semicircle forming the widest part of the body, and being about half an inch distant from the summit of its curve.

The opposite end has the appearance of a quadrate disk (*a*), about $\frac{5}{16}$ inch long; and between this quadrate disk and the semicircular disk just described lies the central portion of the body (*b*) divided into a series of segments. Two pairs of appendages, one large (*2′*) and one (*1′*), small are attached to the extremity of the quadrate disk, while a number of slender limbs are connected with the sides

of the segmented part of the body, the four pairs nearer the quadrate disk being directed towards that end of the body, while the others pass more directly outwards.

The semicircular disk (*c*) is traversed by a strong transverse depression about the middle of its length, which divides it into a wide proximal, and a narrower distal portion. The latter is convex in the direction of the long axis of the body, and presents a little tubercle on each side of the median line close to the transverse depression. The periphery of the distal portion has the form of a curved ridge, separated by a corresponding groove from the rest of the upper surface, and by another groove from the line of junction of the upper and lower surfaces (*e*). On clearing away the matrix as far as was practicable, I found the under surface of this part to be far more convex than the upper, and to present a transverse line apparently indicating the boundary of a segment. In consequence of its convexity inferiorly, this portion of the body has a thickness of as much as $\frac{3}{8}$ths of an inch.

The proximal portion of the semicircular disk appears to be somewhat crushed ; it is divided by two well-marked longitudinal depressions, which converge from the ends of the transverse depression into a central lobe, narrower proximally than distally, and two lateral ones, whose wider extremities are turned in the opposite direction.

The proximal half of the quadrate disk (*a*) presents two convex lateral eminences, separated by a slight depression, which, like the distal half, is obscured by portions of the matrix. The larger lateral appendage (*2′*, *2″*) attached to the distal half, is, on the right side, composed of a short, wide, basal articulation, with which a quadrate joint, produced into a spine at its outer and distal angle, and presenting a convex outer curve, is articulated. Apparently continuous with the under edge of this joint, is a flat, broad plate (*2″*), with an oval, distal contour, and presenting what appear to be traces of a fringe of setæ on one side. Regarding the quadrate joint and this plate as one part, they form a scoop-like scale, $\frac{1}{4}$ inch long by $\frac{1}{8}$ inch wide. Lying in the hollow of the scoop, and articulated either with its base or with the basal joint itself, is a fusiform mass (*2′*) divided by two constrictions into three joints, the middle one being shortest and subquadrate, while the inner and outer are conical. The outermost passes into a cylindrical multiarticulate filament, whose extremity is buried in the matrix. A longitudinal groove furrows the outermost articulation and is continued on to the filament, giving rise to an appearance of division—but I believe this to be accidental.

On the left side the appendage has a similar structure, but is less perfectly preserved.

The small appendages (*i'*) of the quadrate disk lie between the large ones. They consist of two proximal subcylindrical short joints, which do not equal more than half the length of the scale of the outer appendage; beyond these, traces are visible of another joint, and of a long, multiarticulate, terminal filament.

On the one side of the specimen, the matrix comes close up to the edge of the quadrate disk; but on the other, an elongated, narrow plate (*d*), with a somewhat excavated anterior margin, joins it at the base of the scale-like appendage. This plate is exposed for about $\frac{3}{32}$nds of an inch in width and $\frac{3}{8}$ths of an inch in length. Its outer margin is straight, and slopes outwards so that proximally it is $\frac{5}{16}$ths of an inch distant from the axis of the specimen, while distally (or at the base of the scale) it is only $\frac{1}{4}$ inch distant from the same imaginary line. A narrow triangular space, occupied by matrix, is left by the divergence of the plate from the central part of the body, and lodges three of its appendages on this side.

The central part of the body (*b*) measures about half an inch in length; it is narrowest towards the quadrate disk, widest at the opposite extremity, where it attains nearly $\frac{7}{16}$ths of an inch, and is divided into seven segments of nearly equal length, but gradually increasing breadth. Each segment appears to consist of a median plate, separated by an oblique furrow from two lateral plates; the latter are quadrate, with their margins concave outwardly and towards the quadrate disk; convex and somewhat raised, towards the semicircular disk. The median plate increases in width from the segment nearest the quadrate disk, which we may call the first, to the last. The lateral plates are nearly of the same size throughout, except the first pair, which appear to be larger than the others.

Attached to the outer boundaries of the lateral plates, seven appendages are observable on the left side, but only six on the right. In the more perfectly preserved appendages (fig. 1 *c*) there may be distinguished a short, proximal, convex, subcylindrical joint, followed by at least three other slender and delicate articulations; of these the proximal one is the longest, the terminal next in length, and the middle one shortest.

The terminal joint exhibits indications of further subdivision.

The fifth limb on the right side (the left side of the animal, as we shall see) presents a very important character, inasmuch as there lies parallel with and behind it a delicate, curved, many-jointed filament (fig. 1 *c*), which externally abuts against the terminal joint of the

appendage, and internally lies parallel with the longer cylindrical joints, and in close contiguity with the basal division of the appendage. I believe, in fact, that this filament is nothing less than the outer division of the appendage, or its exopodite ; and I am inclined to think that traces of a corresponding filament are visible in some of the other appendages.

No. 2 (fig. 3).—This specimen is the more perfect of the two belonging to Mr. Cooper. Like No. 3, it was obtained from the shale overlying the upper or thick coal-beds of Bilston, and is imbedded in a lighter-coloured ironstone than the foregoing, to which, in other respects, it bears a close resemblance. In fact, it presents precisely the same view of the fossil, and differs from the Manchester specimen chiefly in the absence of the semicircular disk, which is replaced by a deep pit in the relief, with which a corresponding elevation in the cast corresponds. The median part of the body and its appendages are similar to those above described, but the traces of the multiarticulate exopodite are but obscurely exhibited : the quadrate plate is of the same character, but its internal small pair of appendages are hardly traceable, though the external ones (fig. 3, *2''*) are well preserved. The great feature of interest about the specimen is, that there lies on both sides of the quadrate disk a narrow plate (*d*), like that found on the one side only of the Manchester specimen. On the left side this plate does not extend further backwards than the proximal edge of the quadrate disk ; but on the right side it is traceable as far as the fourth segment, and has, lying between it and the quadrate disk, the 1st, 2nd, 3rd, and 4th appendages of its side. On this side also the plate exhibits a slight transverse furrow ending in a small spine at the point marked (*d*). Distally, both narrow plates appear to be continuous with the quadrate disk.

No. 3 (fig. 2).—This specimen is much crushed and distorted, though the segments of the central division of the body, the appendages of one side, and the two scale-like bases of the large appendages of the quadrate plate are clearly visible. The great interest of this specimen proceeds, however, not from the existence of these parts, which are better shown in Nos. 1 and 2, but from the fact that in the place of the semicircular disk we see two broad plates convex from side to side, and a large portion of a third ; all of them being obviously the lateral moieties of large segments similar to that whose boundary could be traced on the inferior convexity of the semicircular disk in No. 1 (fig. 1 *b*, *e*). On one side of the specimen (external to *b*, fig. 2) there lies a plate which probably corresponds with those marked *d* in the other figures.

A glance at the different specimens which have been described is sufficient to convince the investigator of their Crustacean nature; but in endeavouring to make a further step, and to determine the precise order of *Crustacea* to which No. 1 was to be referred, I was for a long time obstructed by the difficulty of deciding which end was the head and which the tail, and whether the surface exposed to view in this and the other specimens was the ventral or the dorsal. At first I was inclined to regard the semicircular disk as a cephalic buckler; and, as the edges of this disk clearly overlap some of the limbs, I was led to think that the dorsal surface was visible and that I had before me a most anomalous form, with a head something like that of an *Apus* or a Trilobite, the thorax of an Isopod, with the limbs of a Schizopod, and with the abdomen and caudal appendages altogether peculiar and anomalous. I was inclined to imagine, therefore, that this singular form combined the characters of several orders of *Crustacea*.

The high palæontological interest attaching to the discovery of such a form, however, led me to give additional weight to every argument adverse to the validity of this provisional interpretation; and, apart from these considerations, there were several circumstances which were great obstacles in the way of this view of the matter. I could not understand the nature of the elongated plate attached to one side of the quadrate disk in No. 1; the supposed caudal filaments were wholly without parallel in the Crustacean series; and I could not see in what part of the body the segments exhibited in No. 3 had their place. Furthermore, the form and apparent annulation of the under surface of the supposed cephalic buckler were quite incomprehensible.

All these doubts were greatly strengthened when Mr. Cooper kindly sent his specimen No. 2 for my inspection, which, exhibiting a flat plate attached to *both* sides of the quadrate disk, clearly proved that the one plate of the Manchester specimen was not a merely adventitious appearance, while the deep excavation at the end corresponding with the hemispherical disk seemed to show that, in this specimen also, the corresponding division of the body was very convex inferiorly. Now I know of no Crustacean possessing a cephalic buckler, in which that region is more convex ventrally than dorsally.

Perplexed by all these doubts, I next reversed my hypothesis; and, assuming the quadrate disk to be the head, the hemispherical disk to be the caudal extremity, and the exposed face to be ventral,—I sought to ascertain whether, by working out the necessary conse-

quences of this supposition, I should not arrive at a result more in accordance with some of the known modifications of the Crustacean plan.

Upon this hypothesis, the small internal pair of appendages to the quadrate disk are antennules ; the large external ones antennæ ; the seven segments are the sterna of seven thoracic somites, increasing in width from before backwards ; the narrow longitudinal plates are the edges of a short carapace ; and the semicircular disk is the termination of a large abdomen bent upon itself, and having its caudal plates flattened out and crushed upon its anterior part. The two and a half segments in No. 3 are, on this hypothesis, nothing but so many of the abdominal somites viewed laterally.

If I had been acquainted with no part of these specimens but the quadrate disk and the segmented central portion of the body, I should have had no hesitation whatsoever in adopting this view of their nature; and even although the assumption that the semicircular disk is the crushed terminal portion of the abdomen may seem somewhat bold, yet it is the sole obstacle in the way of the only hypothesis which enables us to bring this singular form within the category of ordinary Crustaceans.

For if, adopting this theory of the sides and ends of the fossil, we compare it with the little *Mysis* or "Opossum-shrimp" of our own seas, we shall find some curious points of resemblance between the two.

In *Mysis* (fig. 5), as in *Pygocephalus*, the abdomen is very large as compared with the thorax, and the carapace is short and delicate. The antennules (*1'*) present two subcylindrical basal joints ; the antennæ have two large basal joints giving attachment to a large scale (*2''*) externally and superiorly, while, internally, the fusiform base of the internal division of the antennæ is formed by three joints, with the last of which a very long multiarticulate filament is continuous.

There are seven pairs of *conspicuous* thoracic members in *Mysis*, the first pair of thoracic appendages (last cephalic of Milne-Edwards) being smaller than the others and applied against the mouth: so there are seven pairs of appendages in *Pygocephalus*, but the nature of the oral appendages in the fossil does not appear.

In *Mysis* again the thoracic limbs (fig. 4) are short and feeble, and consist of two parts, an endopodite and an exopodite, the latter being terminated by a many-jointed filament. They present the same peculiarities in *Pygocephalus*.

In *Mysis* the sterna of the thoracic somites are well developed and

gradually increase in width from before backwards; so also, on this reading of the fossil, do those of *Pygocephalus*.

The abdomen of *Pygocephalus*, however, is much thicker and stronger in proportion than that of *Mysis*; and its telson and the appendages of the last somite, which together constitute the caudal fin, differ greatly in form from those of *Mysis*, being far wider. The outer edge of the caudal fin again in *Mysis* is nearly straight, while in *Pygocephalus* it is much curved.

In all these respects *Pygocephalus* more nearly approximates to the *Squillidæ*; and I have given a sketch of a *Gonodactylus* bent upon itself, and viewed from the ventral side (fig. 6), as I suppose the fossil to be, in order to show how closely the general proportions of the two genera approximate.

I cannot imagine that all these coincidences are accidental, and I conclude therefore that *Pygocephalus* is a Podophthalmous Crustacean in all probability more nearly allied to *Mysis* than to any other existing form.

At any rate we shall be quite safe in assigning to it a position among either the lower *Decapoda* or the *Stomapoda*[1]; and supposing the interpretation which I have given of this difficult fossil to be well founded, it affords, so far as I am aware, the first certain evidence of the existence of *Podophthalmia* at so early a period as the Carboniferous epoch.[2]

[1] I have elsewhere (Lectures on General Natural History, 'Med. Times and Gazette,' May 23rd, 1857) given my reasons for limiting the group of *Stomapoda* to *Squilla* and its immediate allies. The *Schizopoda*, including *Mysis*, are not essentially different from *Decapoda*.

[2] If the genus *Gitocrangon*, described by Richter (Beitrag zur Paläontologie des Thüringer Waldes, p. 43), really constitute, as its discoverer considers, a transition between the *Macrura* and *Brachyura*, it is not only an earlier, but a more highly organized Crustacean.

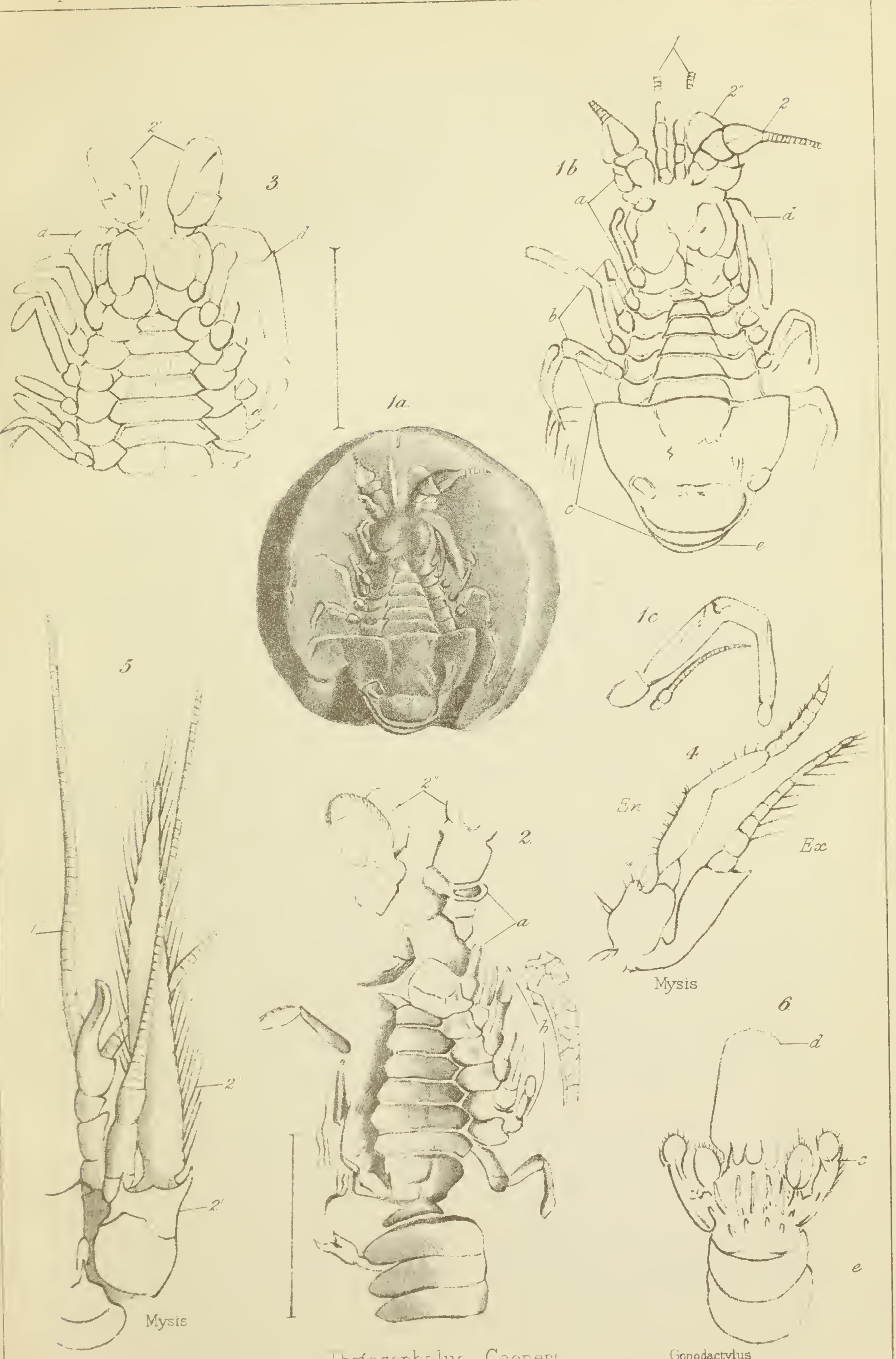
DESCRIPTION OF PLATE XIII. [XXIX.].

Fig. 1 *a*. *Pygocephalus Cooperi*, No. 1 : nat. size. The Manchester specimen.
Fig. 1 *b*. The same : magnified $1\frac{1}{2}$ diameter.
Fig. 1 *c*. Thoracic appendage of the same : magnified.
Fig. 2. Mr. Cooper's specimen, No. 3 : magnified.
Fig. 3. Mr. Cooper's specimen, No. 2 : magnified.
Fig. 4. Thoracic appendage of *Mysis* : magnified.
Fig. 5. Antennule and antenna of *Mysis* : magnified.
Fig. 6. *Gonodactylus* bent upon itself, in outline ; the appendages being omitted : magnified.

a. Quadrate disk.
b. Central part of the body.
c. Semicircular disk.
d. Marginal portions of carapace.
e. Tergal surface of abdominal somites.
En. Endopodite. *Ex*. Exopodite.
1′. Antennules.
2′. Base and inner division of antenna.
2″. Outer division of antenna, or scale.

To face p. 403.

Quart. Journ. Geol. Soc. Vol. XXI. Pl. XIII.



Pygocephalus Cooperi

C. H. Bone del. et lith.

W. West imp.

XLIV

ON DYSTERIA; A NEW GENUS OF INFUSORIA

Quart. Journ. Microsc. Sci., vol. v., 1857, *pp.* 78–82

THE credit of the discovery of the animal which will be described in the following pages is due to my friend Mr. Dyster, of Tenby; and many of the most important statements regarding its structure and habits are based upon his observations. I think, therefore, I cannot do better than name the genus of which it will form the type after him.[1]

The creature was found in swarms among the algæ coating the shells of a *Patella* and of a *Littorina* which had long inhabited a marine vivarium. I had the opportunity of examining its structure when visiting my friend during the past autumn, and the following paper must be regarded as an account of Mr. Dyster's work, with some additions of my own.

Dysteria armata (Pl. VII. [XXX.] fig. 13), has an oval body, $\frac{1}{350}$th—$\frac{1}{250}$th of an inch long, by $\frac{1}{400}$th—$\frac{1}{450}$th broad, which is not altogether symmetrical—the one side presenting a considerable, evenly rounded convexity, while the other, less prominent, is divided by an angulated, longitudinal ridge (*m*, *k*) into a smaller, dorsal, and a larger, ventral area. The edges of both lateral surfaces are sharp and thin; dorsally they are separated by a shallow groove (*n*, *o*), but along the ventral line of the body the groove is deep and narrow, and the produced edges of the lateral parietes (*n o*) resemble the valves of a bivalve shell.

The ventral and dorsal grooves pass into one another in front, but posteriorly the lateral edges are united for a short space (*h*). The edge of the left, less convex, side of the body ends anteriorly in an

[1] Sticklers for classical terminology may however, if they please, derive the name from δὺς and τερας, "a difficult sort of monster," or otherwise, from δύστερις, "perversely disputatious," on account of the controversies to which the obscure structure of the animal may give rise.

obtuse point (*m*), which corresponds with the anterior termination of the angulated ridge, and does not extend, by any means so far forward, as the edge of the right side, which remains thin, and forms the anterior extremity of the body.

At the anterior extremity the large oral aperture (*a*) is seen, just below the angulated ridge and occupying the bottom of a deep fossa, which here takes the place of the dorsal and ventral grooves. The left wall of this fossa is thickened, and projects inwards so as to form a cushion-like lobe, clothed with remarkably long cilia ; and these cilia are continued into the oral aperture itself—the posterior ones being large, usually directed transversely to the axis of the body, and having at times much the appearance of vibratile membranes.

The bottom of the oral fossa is strengthened by a curious curved rod (*l*), which terminates superiorly in a bifid tooth, while inferiorly it appears to become lost in the wall of the fossa.

But there is a much more prominent and easily distinguishable apparatus of hard parts situated on the opposite or ventral side of the mouth, and extending thence through two thirds of the length of the body (*b*, *c*). It consists of two portions—an anterior, somewhat rounded mass, in apposition with a much elongated, styliform, posterior portion.

It is very difficult to assure oneself of the precise structure of the anterior portion (*f*), but it would seem to be a deep ring, composed of three pieces—two supero-lateral and mutually corresponding (*q*, fig. 14), united with a third, inferior, azygos portion (*p*). The latter is somewhat triangular, with a broad base and rounded obtuse apex ; the latter being directed forwards and immediately underlying the oral aperture, while the former is turned backwards, and unites with the two supero-lateral pieces. Each of these is concave internally and convex externally, so as to form a segment of a circle, and presents a clear median space, the optical expression of either a perforation or of a much thinned spot.

The anterior edge of each supero-lateral piece is nearly straight, but the posterior is convex, and it is by this edge that it articulates with or is apposed to, the anterior extremity of the posterior division of the apparatus. Viewed laterally this posterior portion appears to consist of two styles, which are somewhat like nails in shape ; their anterior extremities being truncated so as to present a sort of nail-head, while the posterior extremity seems to take to a fine point. Rather in front of the middle of its inferior edge each style seems to give off a short process downwards (*s*), and this process is, in botanical language, decurrent upon the style. Careful examination of the dorsal or ventral aspect of these parts shows that the decurrent process is in

fact only the expression of a delicate membrane, which is bent so as to have a ventral convexity, and connects together the two styles (fig. 15). It might be said, therefore, that the posterior part of the apparatus is a triangular membrane, deeply excavated in front, bent so as to be convex downwards, and having its margins thickened and produced into styliform enlargements. This curious piece of mechanism is directed upwards and backwards, and terminates in the substance of the body without any apparent connection with other parts.

The whole apparatus is moveable. The posterior portion is pushed against the anterior, and the heads of the styles come into contact with the posterior convex edges of the supero-lateral pieces, and push them forwards ; the posterior portion is then retracted, and the whole apparatus returns to its previous arrangement.

In one *Dysteria*, which had swallowed a filament of *Oscillatoria*, so long, that the one extremity projected from the mouth, when the other was as far back in the body as it could go, these movements took place as many as twenty times in a minute.

Mr. Dyster further informs me that, in one of these animals which he saw feed the frond of *Oscillatoria* was rather "swum upon" than seized, ingestion being accomplished by a smooth gliding motion, apparently without displacement of the styles ; but that when the act was completed the styles "gave a kind of snap and moved slightly forwards."

Mr. Dyster is inclined to think that the *Oscillatoria* passed *through* the anterior ring-like portion of the apparatus. I have not seen the animal feed, but on structural grounds I should rather have been inclined to place the oral aperture at *a*, fig. 13, and to suppose that the food would pass *above* the anterior ring. The apparatus is destroyed by caustic potash, but remains unaltered on the addition of acetic acid ; it is therefore, probably, entirely composed of animal matter.

Immediately above the annular portion of the apparatus, there is invariably present a remarkable amethyst-coloured globule (t), apparently composed of a homogeneous fluid. It has on an average a diameter of $\frac{1}{2000}$ inch, and it is entirely lodged in the more convex portion of the body.[1] In many specimens no other colouring matter than this can be detected, but in some, minute granules ($\frac{1}{75000}$ inch) of a similar colour are scattered through the body. What connection these have with the large constant globule is not clear, since, although

[1] In one or two specimens a minute amethystine globule, not more than one sixth the diameter of the large one, was visible immediately below and behind it. Acetic acid destroys the colouring matter.

the dimensions of the latter vary from the size given above to one fourth or less, no relation could be observed between this diminution and the presence of the granules in other parts of the body.

Behind the amethystine globule the substance of the body has the appearance, common to the Infusoria generally, of a mass of "sarcode," in which the ingested matters are imbedded, and no clear evidence could be obtained of the existence of any digestive cavity with distinct walls.

A little behind the middle of the body, and towards its ventral edge, there is a clear spheroidal "contractile space" (*a*), which varies a good deal in size. One measured $\frac{1}{1500}$th of an inch in diameter, and became entirely obliterated in the contracted state.

The contractions are not rhythmical, but take place irregularly. On the approach of death the space becomes irregularly and enormously enlarged, until it occupies perhaps a third of the whole contents of the body.

Immediately beyond the contractile space there is a curious oval body (*e*), having its long axis ($\frac{1}{5000}$ in.) directed upwards, and containing a comparatively small central cavity, so that it appears like a thick-walled sac.

Indications strongly suggestive of an inferior opening were sometimes observed in this body, but no demonstrative evidence of the existence of any such aperture could be obtained.

The walls of the ventral groove are provided with long and powerful cilia, a remarkably strong one being attached behind the base of the "appendage," and by their means the animal, when free, is propelled at no very rapid rate through the water. Its more usual habit, however, is to remain fixed by means of the peculiar appendage (*f*), and then the cilia act merely in creating currents, by which nutritive matters are brought towards the mouth.

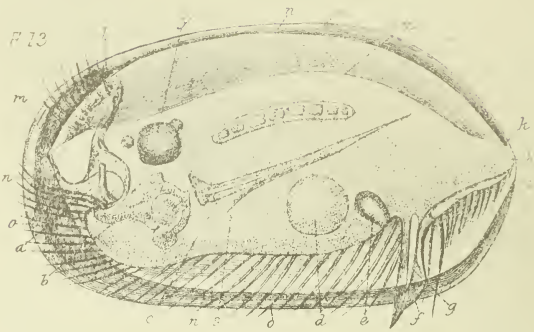
The appendage referred to is attached to the surface of the body, rather towards the convex side, at the bottom of the ventral groove, and is distant about one fifth of the whole length from the posterior extremity. It is $\frac{1}{800}$th to $\frac{1}{1000}$th of an inch in length, and is not altogether unlike a boot, with a very pointed toe, in shape; and the toe appears to be viscid at its extremity, so as readily to adhere to any foreign object. The appendage then forms a pivot on which the whole body turns about, and this appears to be the habitual and favourite position of the *Dysteria*.

Internally, the appendage contains a canal (*g*) wider above than below, and apparently blind at each extremity.

No "nucleus" could be found, though carefully sought for with the aid of acetic acid.

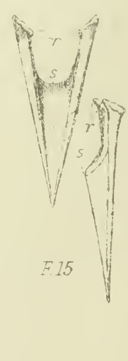
[PLATE XXX]

To face p 408.



F.13

F.14



F.15

The occurrence of transverse fission was noticed very distinctly in one case; but it is remarkable that, notwithstanding the great number of specimens which were observed, no other instance of this mode of multiplication came under the notice of Mr. Dyster or myself. It would appear that the "apparatus" disappears, and is reproduced during fission, for in the single case observed, mere rudiments of it were to be seen in each half of the strongly constricted mass.

Dysteria has not hitherto been observed to become encysted, although this condition has been carefully sought for.

There can, I imagine, be little doubt as to the true systematic position of *Dysteria*. The absence, in an animal which takes solid nutriment, of an alimentary canal with distinct walls, united with the presence of a contractile vesicle, with the power of transverse fission, and with cilia as locomotive organs, is a combination of characters found only in the *Infusoria*. In this class, again, the existence of a sort of shell or *lorica*, constituted by the structureless outer layer of the body; the presence of a submarginal ciliated groove around a large part of the margins of the body; and the inequality of the two lateral halves, leave no alternative save that of arranging *Dysteria* near or in the *Euplota* of Ehrenberg.

Indeed there is one species figured by Ehrenberg ('Infusionsthierchen,' p. 480, pl. 42, fig. xiv.), *Euplotes macrostylus*, found at Wismar, on the Baltic, which, in general aspect, and in the possession of a foot-like appendage, so closely resembles the present form, that were it not for the absence of any allusion to the amethystine globule, or to the "apparatus," I should be strongly inclined to think it identical with *Dysteria*. That an internal armature is not inconsistent with the general plan of the *Euplota*, is shown by *Chlamidodon*, whose apparatus of styles would probably repay re-examination.

Notwithstanding certain analogies which might be shown to exist between the manducatory apparatus of some Rotifera (see *e.g.*, that of *Furcularia marina*, figured by Mr. Gosse, in his excellent memoir, 'Phil. Trans.,' 1846) and the "apparatus" of *Dysteria*, I see no grounds for regarding the latter as in any way an annectant form between these groups.

DESCRIPTION OF PLATE VII. (XXX.]

Fig. 13. *Dysteria armata.*
Fig. 14. Part of mouth of ditto.
Fig. 15. Process between two styles.

XLV

REVIEW OF DR. HANNOVER'S MEMOIR: "UEBER DIE ENTWICKELUNG UND DEN BAU DES SÄUGETHIERZAHNS"

Quart. Journ. Microsc. Sci., vol. v., 1857, *pp.* 166–171

In this beautifully illustrated memoir, Dr. Hannover contributes much interesting information with regard to the histology of the dental tissues in the *Mammalia* generally; but we suspect that both by the author, and by the scientific public, the pith of the essay will be considered to lie in the views respecting the development of the teeth, whose exposition occupies so large a portion of it. It is to these, therefore, that we shall chiefly direct the reader's attention in the course of the following critical analysis. Dr. Hannover commences his work thus:—

"The dental sac of *Mammalia* contains four elements, which, without coalescing, lie in contact, and are distinguishable by their very peculiar structure. Below, on the bottom of the sac and coalesced (verwachsen) with it, lies a soft body, which at a very early period acquires the form of the crown of the tooth. This body is the dentine-germ (dentin-keim); by a process which we shall call 'dentification' it becomes dentine, a substance characterised by the branched tubules which it contains. The dentine-germ is immediately covered by the enamel-germ: this consists of cells (the enamel-cells), on the whole arranged perpendicularly, which are at first very soft, but subsequently, by calcification, become solid columns, and constitute the hardest substance of the tooth—the enamel. Most externally in the dental sac lies the cement-germ, which, by a process of ossification quite analogous to that which takes place in bone, is changed into cement,

characterised by its osteal lacunæ and medullary canals. The cement-germ, however, lies in immediate contact neither with the enamel nor with the dentine, but is separated from them by a peculiar membrane, not yet sufficiently distinguished; this carries upon its inner surface the enamel-cells, which are disposed perpendicularly upon the dentine, and consequently it separates the cement-germ from the enamel-germ; but where the enamel-germ ceases it separates the cement-germ from the dentine-germ. We shall term this membrane the *membrana intermedia;* in the complete tooth it appears as the *stratum intermedium.*" (p. 3.)

The careful study and collation of different passages in Dr. Hannover's work show that his dentine-germ is the dental papilla of English writers; that the enamel-germ is the *membrana adamantinæ;* that his *membrana intermedia* is the layer of what Nasmyth ('Researches on the Development, &c., of the Teeth,' 1849, p. 107) describes as "oval cells," seated on the deep surface of the stellate tissue of the enamel-organ; and that his cement-germ is nothing more than the stellate tissue of the enamel-organ, which he confounds with the vascular "actinenchyma" or peculiar connective tissue of the proper wall of the dental sac.

Under the head of the development of the enamel, Dr. Hannover offers us nothing new; but repeats, without bringing forward new evidence, and as if it had never been disputed, the old view that the enamel is produced by the direct calcification of the columnar cells of the *membrana adamantinæ.* Nor can we find any essential difference between Dr. Hannover's theory of the formation of the dentine and that advocated by Professor Kölliker and others, except that he denies the existence of a *membrana preformativa*, and affirms that—

"This so-called membrane is, in my opinion, nothing but the outermost layer of dentine-cells, in which dentification has just commenced." (p. 12.)

How this can be reconciled with the unquestionable facts that the *membrana preformativa* can be traced with great ease, uncalcified, on to the primary cap of dentine, and that it is a structureless membrane in which no trace of cells has ever yet been detected, we know not; but we are inclined to suspect that Dr. Hannover has never seen the true *membrana preformativa.*

As regards the *membrana intermedia* we are desirous to do Dr. Hannover no injustice in endeavouring to explain, what seems to us to be, his erroneous view of its functions and homologies in the adult tooth, and we will therefore cite his account of it at length.

"4. *Membrana intermedia.*

"I have bestowed this name upon a membrane which has not as yet received sufficient attention.[1] It is a fine and delicate membrane, which must not be confounded with the membranous expansion of the enamel-cells, and which lies within the cement-germ, between it and the enamel-cells. It appears in transverse sections of the germ as a fine white line; is a tolerably firm and opaque membrane, and consists of a structureless mass, in which very numerous small, round or oval, angular or pointed nuclei, without distinct nucleoli, are imbedded. The boundary towards the cement-germ is sharp and linear, and the cells of the cement-germ are pressed against it (fig. 11 *a.*) The boundary towards the enamel-cells, which lie upon the opposite surface, is also well defined (fig. 19 *a.*) The enamel-cells may be detached with tolerable ease, whilst it is only with difficulty that the *membrana intermedia* can be separated from the cement-germ. It is, therefore, best examined in connection with the cement-germ, and, indeed, in the teeth of the new-born infant. In order to observe the attached enamel-cells, the membrane may be folded, because in thin sections the enamel-cells easily fall off.

"The thickness of the *membrana intermedia* differs considerably in dental sacs of different ages. In the persistent teeth of the new-born infant it is hardly visible to the naked eye; in their milk-teeth it is very easily recognisable, in consequence of its white colour, and has considerably increased in thickness; it is thickest, perhaps, about the constricted part or neck of the dentinal germ, with which it is also more intimately connected. Fig. 19 *a* shows its thickness in the deciduous molar of a new-born infant.

"The *membrana intermedia* does not belong to the crown or the enamel alone, for it is continued uninterruptedly upon the fang, here separating the dentine from the cement, and, as in the crown, lying upon the inner surface of the cement-germ. However, I have not been able to demonstrate it here, in an isolated form, because immediately on the formation of the outermost layer of dentine, it coalesces with it, and can be recognised only from its appearance in the complete tooth, where we shall find it as the *stratum intermedium.* If we consider the *membrana intermedia* as a whole, it may be regarded as a sac-like structure which is inclosed within the dental sac, so that the cement-germ is situated between the *membrana intermedia* and the

[1] Kölliker has, perhaps, figured it in his 'Mikroskopische Anatomie,' p. 99, fig. 211 *d*, without, however, recognising its true nature. What Tomes has termed "basement membrane" appears to have been not exclusively the *membrana intermedia*.

dental sac ; perhaps the membrane becomes reflected over the inner surface of the dental sac."

Now there can be no doubt as to the existence of this layer. It was, as we have seen, described by Nasmyth ; it is, as Dr. Hannover justly states, figured by Professor Kölliker ; and we have repeatedly seen it ourselves without feeling inclined to lay any very particular stress upon its existence. If there is any advantage in calling it *membrana intermedia*, we shall be happy to adopt this term. But we must demur to Dr. Hannover's view of its ultimate fate, as contained in the following passage (p. 110) of his memoir.

"4. *Stratum intermedium.*—The nucleated membrane, which during the development of the tooth is closely united with the cement-germ, and serves for the attachment of the nucleated end of the enamel-cells, and to which we have given the name of *membrana intermedia*, is always sufficiently obvious in the perfect tooth, though much changed. It receives its persistent form only after the enamel-cells are calcified throughout their whole length ; since it lies between the enamel-cells and the cement, the ossification of the cartilaginous cement-germ can only take place after the completion of the development of the *membrana intermedia*. Hence in the crown it always separates the enamel, in the root, the dentine, from the cement. Since, however, the cement-germ as a rule does not ossify, but becomes abortive on the crowns of teeth with conical dentine-germs, the *membrana intermedia* in such crown lies free, and in teeth which have not been worn forms what Kölliker terms the cuticle of the enamel."

Dr. Hannover then goes on to speak of the identity of his *stratum intermedium* with the "persistent capsule" of Nasmyth ; and he describes the mode of raising up the membranous *stratum intermedium* in young teeth, by the action of dilute acids, which he states to have been discovered by Erdl in 1843.

Dr. Hannover appears to be unaware that this persistent capsule, or "Nasmyth's membrane," has of late been the subject of special investigation on the part of Professor Huxley, M. Lent, and Mr. Tomes, and therefore he does not attempt to meet the obvious objections which an acquaintance with the known relations of Nasmyth's membrane in the young dental sac would have suggested. Inasmuch, in fact, as Professor Huxley's statement, that Nasmyth's membrane lies on the inner side of the cells of the *membrana adamantinæ*, between these and the fibres of the enamel, has been confirmed both by M. Lent and by Mr. Tomes, it will probably be admitted to be correct ; and consequently the *membrana intermedia* of Dr. Hannover, which lies *outside* the cells of the *membrana adamantinæ*, and is separated by

their entire length from Nasmyth's membrane, can have nothing to do with the latter. In fact, we believe that the "*membrana intermedia*" is an entirely transitory epithelial structure, and enters in no way into the composition of the tooth.

We must express the same opinion with respect to the "stellate tissue"—Dr. Hannover's cement-germ. Dr. Hannover, after giving an account of the early changes of the epithelial lining of the dental sac, and the production of the stellate cells, in a manner not essentially different from that contained in Mr. Nasmyth's last work, seems to us to make the mistake which has already been committed by more than one writer on these subjects, of supposing the actinenchyma of the thickened wall of the dental sac to be a later stage of the stellate epithelial tissue—with which it has nothing to do, and from which it is separated by the basement membrane of the dental sac. We have in our possession figures, drawn long ago, of sections of the thickened wall of the dental sac, in all essential respects corresponding with Dr. Hannover's fig. 13; and having worked carefully over the relations of the actinenchyma (which is nothing but such connective tissue as may be met with in any soft young organ), with the stellate tissue, we venture to speak positively on this question.

If the cement then is really developed within the actinenchyma, as Dr. Hannover describes it to be, the establishment of the fact will simply prove that his "cement-germ" (*i.e.*, stellate tissue of enamel-organ) has as little to do with the cement, as the *membrana intermedia* has with the *stratum intermedium* or Nasmyth's membrane.

It may be worth while, before concluding this notice, to consider in a few words the present state of our knowledge of the development of the teeth.

In an essay published in this Journal some years ago (vol. i., p. 149), Professor Huxley endeavoured to prove that all the dental tissues, whether cement, enamel, or dentine, are developed beneath the basement membrane of the dental sac, which, on the dental papilla itself, has received the name of *membrana preformativa*; and that the so-called enamel-organ—consisting from within outwards of the *membrana adamantinæ* the *membrana intermedia* of Hannover, the stellate tissue, and the deep layer resembling the *membrana intermedia*, next the basement membrane of the sac—was to be regarded as a transitory epithelial structure, which has as little connection with the development of the tooth as the various modifications of the epithelium of the root sheath of a hair have with that of the shaft of the hair.

Evidence was offered, 1st, that the enamel-fibres, from their first appearance, lie beneath Nasmyth's membrane. 2dly. That Nasmyth's membrane is continuous with the *membrana preformativa*. 3dly. That no traces of cells or endoplasts can be discovered within the enamel-fibres nor in the dentine, and that these tissues are not produced by the direct calcific conversion of pre-existing elements. 4thly. That the cement is morphologically the continuation of the enamel, but whether it is or is not developed by conversion from the pulp was left an open question.

The first of these statements has received full confirmation from subsequent observers, including M. Leydig, in his recently published valuable 'Lehrbuch d. Histologie,' p. 291.

The second assertion has been confirmed by M. Lent, and is not directly controverted in Mr. Tomes's paper on the Development of the Enamel, published in the 15th number of this Journal.

The third statement appears to be justified whenever writers on this question state what they have observed, and not their conclusions from their observations. We are not aware that any one has as yet absolutely seen endoplasts or their remains in distinctly formed or forming enamel or dentine.

Mr. Tomes, in the excellent essay we have cited, endeavours to prove that Nasmyth's membrane is formed by the union of the ends of the cells of the *membrana adamantinæ*, which coalesce into a membrane; and this view would undoubtedly relieve one of much difficulty in understanding the formation of the enamel, and would bring it nearly into the same category as that of molluscan shell; but until it can be shown that Nasmyth's membrane is not continuous with the *membrana preformativa*, and is not an alteration of it, we must adhere to the view that the enamel is, like the dentine, formed under the *membrana preformativa*. Hitherto no one has attacked this side of the argument, nor has the evidence derived from the obvious continuity of the *membrana preformativa* over the whole surface of the teeth in fishes and *Amphibia* been in any way shaken.

XLVI

OBSERVATIONS ON THE STRUCTURE OF GLACIER ICE

Phil. Mag., vol. xiv., 1857, *pp.* 241–260

THE GOVERNMENT SCHOOL OF MINES,
JERMYN STREET,
September 14, 1857.

MY DEAR TYNDALL,

In the following pages I have given you some account of the experiments and observations upon the structure of glacier ice, which, at your suggestion, I commenced during our sojourn at the Montanvert this autumn. No one knows better than yourself how much these subjects grow under the hands of the inquirer, and how little claim my brief investigations have to the character of completeness. Nevertheless my conclusions, so far as they go, are based on such clear and decisive evidence, and are so totally opposed to the views entertained by the highest authorities, that I feel I shall be doing more good by publishing than by withholding them.

I will in the first place state what I have myself observed with regard to the structure and the permeability of glacier ice, and afterwards I will compare my results with those which have been arrived at by others.

Structure of Glacier Ice.—A mass of ice freshly extracted from any part of the Mer de Glace, the Glacier du Géant, or the glacier of La Brenva, at a depth of 8 or 10 inches from the surface, always presented the following characters when examined either with the naked eye, or with a lens of a magnifying power of thirty or forty diameters.

It broke with a vitreous fracture ; and when the surface was made even, either with a sharp knife, or by rubbing on a warm surface, it

appeared perfectly smooth and glassy, exhibiting not the least trace of fissures. Minute shallow pits, however, were scattered over it, and became particularly obvious when a coloured fluid was poured on to the surface and then wiped away again, inasmuch as under these circumstances every pit retained a very small portion of the colour.

The mass was, as usual, traversed by a larger or smaller number of parallel blue veins (whose lenticular form was almost always very apparent, particularly in the Brenva); and when a thin section was made perpendicular to the plane of the veins and viewed by transmitted light, it became obvious that the ice formed one continuous mass, without fissures or interruptions of continuity of any kind. It contained, however, a multitude of small, closed, and perfectly distinct chambers, and it was to the absence or rarity of these in the course of the veins that the latter owed their transparency and blueness.

The form and contents of these chambers were exceedingly remarkable. In a blue vein, and in those parts of the intermediate "white ice" which were contiguous to a blue vein, they were always round or oval disks, with extremely flat and closely approximated sides; so that, viewed in one plane, they looked like circles; but in a plane at right angles to this, like narrow parallelograms. In the white ice midway between the blue veins, on the other hand, I very generally noticed an irregularity of form, which was in many instances so great that the cavities appeared to be ramified. The walls of the chambers very frequently appeared to be a little roughened, or, as it were, frosted.

Every chamber, without exception, which I carefully examined contained both water and air. The former was commonly present in larger quantities than the latter, which swam as a bubble in the water, and could very often be made to move about in the chamber like the bubble of a spirit level. It seemed to me, though I will not pretend to lay it down as a rule, that the air was more abundant in proportion to the water in the more irregular chambers. Where the air was in large proportion to the water, the bubble of course became more or less completely supported by the walls of the containing cavity, and to a certain extent assumed its form; but where, as in the majority of cases, the air-bubble was small in proportion to the water, its figure was spheroidal, and totally different from that of the containing cavity. I mention this particularly, because, as I shall show below, the chambers (which for distinction's sake I will term the "water-chambers") have been confounded with the air-bubbles, and the form

which is characteristic of the one has been erroneously ascribed to the other.

I had no means of measuring the dimensions of the water-chambers, but at a guess I should say they varied from a tenth to a fiftieth or a sixtieth of an inch in diameter.

The line of contact of the water in the water-chambers with the ice was optically perfectly well defined, and easily distinguishable. Hence I have no hesitation in saying, that if canals or fissures of any appreciable size filled with water had existed in the ice, I must, with the magnifying power employed, have discovered some trace of them ; but I repeat, nothing of the kind was discernible in perfectly fresh ice.

If the existence of fluid water dispersed through its substance in closed chambers is shown by future observations to be a universal character of glacier ice (and I cannot imagine that a structure universally prevalent in the Mer de Glace, the Géant, the Brenva, and, as I shall show by-and-bye, from M. Agassiz's figures, in the Aar glacier also, is a mere local peculiarity), it appears to me to be a fact of primary importance. For what I have described is the structure of the unchanged ice of the glacier—of ice which has been protected from the solar or atmospheric influences by that which covered it ; and it must be remembered that the ice which is within a foot of the surface on the Mer de Glace opposite the Montanvert, must have formed a part of the very depths of the tributary glaciers. In other words, the ice which is at this moment, say a hundred feet below the surface in the Glacier du Géant, will, in consequence of ablation, form the superficial ice of some part of the Mer de Glace years hence. Consequently, unless it can be shown that the substance of a glacier, as it approaches the surface, is exposed to some influences capable of developing the water-chambers and their contents, it is to be presumed that the structure found near the surface in the lower part of a glacier is the structure which prevails throughout the thickness of the higher part ; and hence that the structure described is that of unaltered glacier ice in general. This conclusion, as I shall immediately show, is directly confirmed by the boring experiments and by the figures of M. Agassiz.

M. Agassiz's deductions, however, are totally at variance with mine ; and he is so generally quoted as an authority in these matters, that I feel compelled, however unwillingly, to enter into a detailed criticism of his views, which are contained in the following extracts from his 'Système Glaciaire,' numbered, for the sake of more convenient reference, in successive order.

(1) "At its origin, near the Névé, the compact (or proper glacier ice) contains, like the ice of the Névé, a notable quantity of air. But there is this difference between the two, that in the compact ice the air, instead of being distributed through the whole mass, is united in small perfectly circumscribed bubbles, whilst the interspaces of these bubbles are perfectly transparent, so that without being as diaphanous as ordinary water-ice, the compact ice has not the opacity of Névé ice. Moreover, it is more compact, and what is especially characteristic, it presents no trace of granular structure: a fragment exposed to the action of heat does not become resolved into grains of Névé, but breaks up into angular fragments.

"This difference of structure is accompanied by a greater impermeability; water no longer traverses the mass with the same ease and uniformity, but is seen to follow in preference certain angular routes which are the capillary fissures."—P. 151.

(2) "The means employed by nature to maintain this amount of plasticity and compressibility in glacier ice is the water which circulates throughout the mass, and which, while it lubricates it, contributes to maintain within it a constant temperature during the greater part of the year."—Pp. 152, 153.

(3) "*Superficial fissures which must not be confounded with the capillary fissures.*

"When during a fine summer day one travels over the upper regions of the compact ice (about the region of the Abschwung, on the Aar glacier), a continual crepitation is heard on all sides. It is caused by the bubbles of air which on approaching the surface escape through the ice, where they have been dilated by the effect of diathermanicity, and cause the parietes of the ice to burst when they are no longer sufficiently strong to resist the dilatation of the air."—P. 153.

(4) "The air-bubbles undergo no less curious modifications. In the neighbourhood of the Névé, where they are most numerous, those which one sees at the surface are all spherical or ovoid; but by degrees they begin to be flattened, and near the end of the glacier there are some which are so flat, that they might be taken for fissures when seen in profile. The drawing, pl. 6, fig. 10, represents a bit of ice detached from the gallery of infiltration. All the bubbles are greatly flattened. But what is most extraordinary is, that, far from being uniform, the flattening is different in each fragment, so that the bubbles, according to the face which they offer, appear either very broad or very thin. I know of no more significant fact than this, since it demonstrates that each fragment of ice is capable of undergoing

in the interior of the glacier a proper displacement independently of the movement of the whole."—P. 167.

(5) "The same flattening of the bubbles is found at a greater depth. While engaged in my boring experiments, I observed attentively the fragments of ice brought up to the surface by the borer. I found in them almost flat bubbles, perfectly similar to those of the fragment figured above, at all depths from 10 to 65 metres. I observed, besides, that in the fragments which proceeded from a great depth, all the bubbles without exception were strongly flattened, whilst at less depths there were some less compressed and even altogether round, as at the surface.

"It follows, hence, that a strong pressure is exercised in the interior of the glacier."—P. 167.

(6) "I ought also to mention a singular property of these air-bubbles, which at first was very surprising, but afterwards admitted of very satisfactory explanation. When a fragment containing air-bubbles is exposed to the action of the sun, the bubbles insensibly enlarge. Soon, in proportion as they enlarge, a transparent drop shows itself on some point of the bubble. This drop in enlarging contributes its share to the enlargement of the cavity, and as it progresses it predominates over the air-bubble. The latter then swims in the midst of a zone of water, and incessantly tends to reach the most elevated point, at least if the flatness of the cavity does not hinder it."—Pp. 167, 168.

(7) In a note appended to this passage, M. Agassiz speaks of the irregularity of the walls of some of the bubbles, and adds, "The same effect has been produced upon the bubbles of the fragment fig. 10. There also all the bubbles have enlarged by diathermanicity, and a little drop has developed in the middle of each. But as the cavities are very small, the drops do not yet move freely in their cavity."

It will be observed that in Nos. 1, 4, 5, 6, M. Agassiz confounds together the water-chambers and the air-bubbles under the common term of "bubbles," and he affirms (6) that the presence of water in the "air-bubbles" is the effect of exposure to the sun's rays, and of the different diathermanicity of air and ice.[1] A careful analysis of M. Agassiz's facts, however, is very instructive. In the first place, I recognise in his fig. 10, pl. 6, a fair, though rough and sketchy, representation of the general arrangement and form of the water-chambers with their contained air-bubbles The chambers are as usual flattened, but the artist has rightly represented their contained air-bubbles as

[1] The Messrs. Schlagintweit (*Untersuchungen*, p. 17) adopt Prof. Agassiz's views on this point, and with him regard the presence of water as a local and partial phenomenon.

spheroidal. The strangest thing is, however, that M. Agassiz has taken the air-bubbles for drops of water, and the drops of water for air-bubbles, as any one who is familiar with the microscopic appearance of bubbles of air will see, on comparing the description in (7) with the figure 10. In the next place, I repeatedly exposed thin plates of ice to the sun, carefully watching the air-bubbles, without being able to observe the phænomena detailed by M. Agassiz in (6) ; and I must frankly confess I do not understand how such changes as those described are reconcileable with the commonest properties of ice and air. How do the bubbles enlarge when exposed to the sun ? M. Agassiz has already admitted that the chambers are closed (1), and we know that ice is not readibly distensible ; and therefore I hold it to be impossible that the bubbles should visibly dilate before the melting of the adjacent ice ; and as to enlarging by the melting of the ice-wall, the fractional difference between the volume of water and the ice from which it proceeds, would be wholly imperceptible on such a scale. With regard to the explanation of the crackling noise given in (3), I can only say that I have repeatedly watched a thin lamina of ice melting, both by transmitted and reflected light, and that I have seen the walls of the chambers reduced to the thinnest pellicle without being broken by pressure from within. The air-bubbles escape quite quietly as soon as their wall is perforated. Furthermore, the cavities left where the air-bubbles have been, are not fissures at all, but, as I have said above, rounded pits. Indeed, this is a necessary consequence from M. Agassiz's own statements with regard to the shape of the bubbles.

M. Agassiz affirms in (5), that ice brought up from a depth of 65 metres was perfectly similar in structure to that represented in his figure 10. The fact is important ; but surely it alone affords sufficient evidence that "diathermanicity" has nothing to do with the formation of the cavities and their watery contents. And indeed in (4) this same piece of ice (fig. 10) is said to have come from the "gallery of infiltration," a cavity perfectly shaded, and bored many feet below the surface of the glacier. So that either this figure does not represent the structure of the glacier at this point, or the structure is unaltered, and diathermanicity has nothing to do with it.

It follows, therefore, that there is no evidence to show that the influence of solar radiation has anything to do with the structure ; on the contrary, M. Agassiz's *facts* strengthen my case.

If it be the universal character of glacier ice to be full of closed cavities containing fluid water and air, it becomes a matter of extreme interest to ascertain how the air and the water come there ; how it is

that the water retains its fluidity, and how it is that the water-chambers are compressed. It may seem a common-place comparison, but the ice and its cavities containing water remind me of nothing so much as a Gruyère cheese, in which one so often meets with closed cavities containing fluid and air. Let the Névé represent moist curds and the glacier valley the cheese-press, and the analogy is perhaps closer than it looks. But these are questions for you to solve; and I will only venture on one other supposition, viz. that the water-chambers have the value of a register thermometer, indicating that the minimum temperature to which the mass of a glacier descends is never for long less than 32°; otherwise I cannot conceive how the water should remain fluid; and if it were once frozen, how could it melt again?

M. Agassiz makes a very important observation in (4), and one which I am glad to be able to confirm in the main. I took some pains to ascertain the general direction of the planes of the water-chambers, and I found that in the substance of the blue veins they were sometimes parallel to the plane of the latter, while in the white ice their planes were always more or less inclined to the veins, usually forming an acute angle, and never, so far as I have seen, a right angle with them. Furthermore, as Prof. Agassiz points out, the water-chambers are arranged in groups, all the members of the same group having parallel planes, while their direction is more or less inclined to that of neighbouring groups. It seems to me very probable that, as Prof. Agassiz suggests, the different directions of the planes of the cavities may indicate internal changes of place of segments of ice corresponding with the groups; but, as I have already said, no fissures separating these segments are to be found in the deep ice of a glacier, and hence we cannot with propriety speak of them as "fragments."

Such is the structure which I have found to obtain in all "deep" glacier ice, by which I mean, all ice situated more than a few inches below the surface. It is as solid as glass or marble, and as devoid of any but accidental and gross fissures. The glacier, however, where exposed to the atmosphere, presents what may be called a "superficial layer" of very different character. Every one who has had occasion to cut an escalier, must have been struck with the difference between the resistance to the ice-axe at the first blow and that at the fourth or fifth. At the first, the jar to the hand is slight, and fragments of ice fly in all directions; but at the last, one might almost as well be hewing some hard though splintery wood. The reason of this at once becomes apparent on examining the superficial ice. It is com-

posed of larger or smaller granules of exceedingly irregular form,[1] separated by very obvious fissures, but nevertheless so fitted into one another as to cohere with some firmness. The distance to which the fissures extend into the interior of the glacier (and hence the thickness of the superficial layer) varies a good deal ; 7 or 8 inches is perhaps rather above than below their average depth ; but however this may be, the important fact is, that whenever you clear away the superficial layer, you find beneath it what I have termed "deep" ice—that is, ice in which neither fissures nor granules are discernible ; ice which tends to split parallel to the veins, and shows no disposition to break up into the angular fragments so characteristic of the superficial layer.

It has been said that mere optical examination is insufficient to disprove the existence of fissures in the deep ice, and that such fissures are present, though invisible in consequence of being filled with water. I have already shown that the line of contact of water and ice is optically well marked, and that there is every reason to believe that even the finest fissures would be visible under a sufficient magnifying power ; but those who maintain the porosity of glacier ice, rest chiefly on the results of experiments made with coloured fluids. It is said that glacier ice becomes infiltrated throughout its substance with extreme readiness, the coloured liquid traversing fissures which are more particularly developed in the course of the blue veins. It became necessary, therefore, to repeat these infiltration experiments ; and for this purpose, as you will recollect, I made use of the logwood infusion which you had prepared, and which by its combined clearness and intensity of colour was excellently fitted for the object in view.

If a little of the infusion were poured upon the natural surface of the glacier, it immediately soaked in, spreading itself in all directions between the granules (but more rapidly, as I often observed, in directions parallel with the veins), and staining the whole thickness of the superficial layer. Whatever quantity might be poured on to the surface, however, it penetrated no further than the superficial layer (unless there were some obvious crack in the deeper ice) ; and when the latter was cleared away with the axe, and the surface of the deep ice washed or even carefully rubbed with the hand, not a trace of the infusion could be found in it.

If a piece of the deep ice containing several blue veins were allowed to soak in the logwood infusion until it nearly melted away, it remained unstained, and either wiping it or passing it quickly through clean water rendered it perfectly clear and stainless.

[1] The superficial layer is particularly well described by the Messrs. Schlagintweit in their *Untersuchungen über die physikalische Geographie der Alpen*, 1850.

But it is said that if cavities be made in the glacier and filled with a coloured infusion, the latter will soon, by means of the capillary fissures, infiltrate the surrounding mass. To determine this point, I selected a spot upon the north wall of a crevasse, just opposite the Montanvert, and between the centre and the west shore of the Mer de Glace, where the veins were well developed, their planes having a general north and south direction, but dipping at an angle of about 70° towards the centre of the glacier. On the northern aspect of the ice I cut away the superficial layer, so as to form two faces of a cube of about a foot in the side on the deep ice. One of these faces looked westward, and was consequently nearly parallel to the cleavage ; the other looked northward, and was therefore nearly perpendicular to it. Perpendicular to the west face, and therefore to the structural planes, I bored a hole with an auger, about an inch in diameter and 9 inches long, and just sufficiently inclined to the horizon to hold the infusion of logwood, with which I filled it. I then thinned away the north face of the cube very carefully until the north wall of the hole was less than 2 inches in thickness—until, in fact, I could see the dark fluid through the substance of the several blue veins which it traversed with perfect distinctness.

For two hours not the slightest trace of leakage or infiltration into the substance of the ice forming the walls of this cavity could be observed ; and the contour of the contained liquid remained perfectly sharp and well defined. It then began to leak at one point near its upper end through a small crack *in the white ice*, which led directly outwards. The liquid spread neither up nor down in the crack Four hours afterwards no change whatever had taken place in the liquid contained in the lower part of the hole. At this time you joined me upon the ice, and you will recollect that I carefully thinned away the wall with a sharp knife until in some parts it was not more than $\frac{1}{4}$ of an inch thick. Still no infiltration occurred. The knife at length accidentally penetrated the wall, and the liquid at once flowed out. I then poured some clean water through the hole, and all trace of the coloured infusion was at once so thoroughly removed, that, on cutting away one wall, the other appeared perfectly clean and of its natural aspect.

I have given the details of this one experiment in order to show in what manner all were made ; but it is unnecessary to be equally prolix with regard to the others. Suffice it to say, that, whether the holes were bored perpendicular to the structure or parallel with it, or at any intermediate angle, whether in white ice or in a blue vein, the result was precisely the same, not a particle of fluid making its way into the surrounding substance of the ice along the veins, nor in most

cases in any other way. Occasionally a leakage would take place in the manner described above, but the fissures in these cases were gross and visible, and their direction had no reference whatsoever to that of the structure. Indeed, as the leakage always took place towards the surface, and not into the depth of the ice, I am inclined to think that these cracks were produced in cutting the ice to thin away the outer wall of the cavity.

I repeated these experiments in the neighbourhood of the Grand Moulin; on the Moraine du Noire, somewhat higher than the Couvercle; and on different parts of the Glacier du Géant, and everywhere with similar results. Furthermore, having carefully bored a vertical hole in the deep ice of the Mer de Glace, opposite the Montanvert, I filled it with the infusion, and having covered over the aperture with a roof of ice-blocks, I left it until the next morning. It rained hard during the night; and on revisiting the spot after an interval of about fifteen hours, I found that the covering blocks had slipped off, and that the liquid occupied only about the lower two-thirds of the cavity. No trace of infiltration could be discovered; but the lower part of the cavity had changed its figure from cylindrical to irregular and botryoidal. I conceive that the sinking of the fluid must be accounted for by the enlargement of the cavity consequent upon this botryoidal excavation of its walls; and I suppose that the ice-blocks proving an insufficient shelter, the rain poured into the hole, and keeping up a constant supply of comparatively warm liquid, eroded its walls in the way described. However this may be, the fact that the liquid had produced a fresh surface for itself, is important, as it shows that the absence of infiltration through the veins intersected by the cavities containing the coloured infusion is not dependent on a condensation of their walls by the auger.

To eliminate any error of this kind, however, I took a small block of the deep ice, and with a sharp knife fashioned it into a cup, whose walls varied in thickness from $\frac{1}{4}$ to $\frac{3}{8}$rds of an inch. Filled with the infusion and surrounded with ice, this cup remained for two hours without showing a trace of infiltration along its structural planes.

I can only conclude from these experiments, that the chief substance of a glacier is as essentially impermeable as a mass of marble or slate; and that though it may be traversed here and there by fissures and cracks, these no more justify us in speaking of glacier ice as "porous," than the joints and fissures in a slate quarry give us a right to term slate porous. We do not call iron porous because water runs out of a cracked kettle.

The extreme porosity of what I have termed the "superficial

layer," however, is no less certain, and inasmuch as this layer is continually and rapidly wasting away at its surface, it must be as constantly reformed from the solid glacier ice beneath.

The fact observed by Prof. Agassiz, that under a moraine (that is, where covered and protected by stone and gravel) the superficial ice is of the same character as the deep, suggested the idea that the superficial layer is the result of the operation of atmospheric influences; and that just as a bed of impervious rock becomes broken up into fragments, separated by permeable interstices, down to a certain depth wherever it is exposed to the atmosphere, so the glacier ice when left unprotected undergoes a similar weathering and disintegration. I submitted this notion to the test of experiment in the following way:—Not far from the upper end of the Moraine du Noire, and on one bank of a stream which cuts its way down the Glacier du Géant, I cleared away the superficial layer and cut out a block of the deeper ice, which was then divided into two equal portions of irregular cuboidal form, and about 8 inches in the side.

The logwood infusion was poured on both of these, and was retained only by such portions of the superficial layer as had been allowed to remain. Water poured on to the blocks ran off them as it would run from marble or glass, sinking only into the remains of the superficial layer. I then placed the two blocks side by side, on an elevated ridge of the glacier, with their natural upper faces turned towards the sun, at this time (1.15 P.M.) shining brightly; the one block I left without protection, while the other was just covered by a stone of 4 or 5 inches in thickness, resting upon its upper face. At 1.40, that is to say in less than half an hour, I removed the block of stone and poured the infusion over both pieces of ice. The covered one could be as little infiltrated as before, while the face of the uncovered became at once beautifully injected, the fluid instantly running into a network of little superficial fissures which had developed themselves, and out of which the infusion could be only partially extracted by washing.

Both pieces of ice were well washed, and the stone was replaced on the one, while the other was left uncovered as before.

In the course of the ensuing half-hour I examined both blocks several times. The covered ice remained unchanged; but in the uncovered, the fissures extended further and further into the mass, which gradually assumed throughout the granular aspect of the superficial layer. Water poured on its surface soaked into it immediately, and a small quantity of the infusion spread out, the moment it reached the block, in the most beautifully ramified figure through the fissures. Particularly large and apparent fissures could thus be

frequently observed traversing the middle of the blue veins. At length the fissures extended completely through the mass, which thus became truly sponge-like. Water poured on its surface, filling the interstices, gave the mass a clear and semitransparent aspect, though by no means to be compared to that of a blue vein. But as soon as the supply of water ceased, the fissures of the side uppermost immediately began to lose their water, which drained away below, and becoming filled with air, a whitish opaque hue succeeded. On reversing the block suddenly, what had been its under surface appeared at first clear, but the water soon deserting it, it rapidly whitened, while the previous upper and white surface became clear. Water poured upon the upper surface, traversed the mass and flowed out again below with the utmost ease. In fact it is impossible to conceive any more striking contrast in these respects, than that between the freshly extracted ice-block (or that which had remained under cover) and that which had been exposed.

So far as it may be permissible to draw a conclusion from the few experiments I made, I should say that direct exposure to the sun has much influence on the rapidity of this process of weathering ; but it is by no means essential, for the northern faces of the walls of crevasses exhibit a well-developed superficial layer ; and I have seen it even beneath huge boulders, where these were not in direct contact with the ice.

But one conclusion appears to me to be deducible from these experiments, and that is in perfect accordance with the results of ocular investigation. Glacier ice is essentially devoid of all pores, fissures and cavities, save the closed water-chambers ; though of course, like all other brittle bodies, it is liable to become fissured and fractured by pressure from without. Fissures and cavities produced in this way, however, are accidental and not essential. But it is a remarkable feature of glacier ice, that it is liable to weather in a peculiar manner, becoming fissured and breaking up into irregular fragments to a certain depth. The superficial layer formed in this way is eminently porous, and absorbs fluids like a sponge.

In arriving at these results, however, I again regret to find myself in direct opposition to the current doctrine based on the statements of Prof. Agassiz, from whose 'Système Glaciaire' I continue my series of quotations.

(8) "*Capillary fissures.*—The true capillary fissures are very different from the superficial fissures which have just been described (3). They exist not merely at the surface, but are found on the walls of crevasses and in the interior of cavities where the rays of the sun

never penetrate. They are larger than the little fissures which have just been mentioned, and far less numerous, particularly in the regions in which the latter abound. Their distribution is not uniform in the interior of the compact ice," p. 154 ; but (M. Agassiz goes on to explain) they are arranged in bands and zones, which, becoming more completely infiltrated with water than the intermediate ice, appear blue and transparent, and are the blue veins.

(9) " The quantity of bubbles with which the white ice is filled, is the reason why the fissures are more slowly propagated in it ; the air, by its elasticity, being unfavourable to the formation of fissures (l'air qui est de sa nature élastique ne favorisant aucunement le crevassement). By degrees, however, and in proportion as the infiltration perpetuates itself, the rigidity increases, and the fissures multiply in proportion. Every bubble that a fissure meets in its course loses its aëriform contents. It becomes transparent, and the opacity of the mass is so far diminished. The consequence of this multiplication of fissures is continually to diminish the number of bubbles, and by this means to render the ice more and more transparent and blue.

" It will be evident to any one who has followed the progress of modern physics, that this phænomenon is due solely to the diathermanicity of ice. The air first and then the water becomes heated through the ice. However minute may be the degree of heat which is thus transmitted to them, it is enough to melt a part of the ice which surrounds them, and thereby to increase the cavity in which they are imprisoned. I do not think, however, that any very great importance should be ascribed to this phænomenon ; and the fact that it is produced only when the ice is exposed directly to the rays of the sun, is in my eyes an indication that it exercises no notable influence on the mechanism of glaciers."—P. 157.

(10) " When the ice has acquired a certain degree of transparency, and the network of capillary fissures is fully established in it, water and air penetrate into the fissures with great facility. One may assure oneself of this in many ways, among others by the following experiment, which I have repeated many times. Let a cube of ice of a few decimetres on the side be detached from the bottom of a crevasse, in that part of the glacier where the ice is most transparent, and placed upon a rock. At first, a few fissures will appear on the surface, then these fissures will be gradually propagated into the interior, and the network becoming more and more complex, will by degrees reach the base. If, then, the block of ice be turned upside down, and water be poured upon it, all the fissures will disappear from above downwards, in the same order as they were formed. The block will remain

perfectly transparent so long as it is saturated; but so soon as one leaves off watering, the fissures reappear where they last appeared when the block was reversed."—P. 161.

(11) "The angular fragments are the consequence and the product of the capillary fissures. When a morsel of compact ice is exposed for some time to the air, it becomes decomposed into a certain number of angular fragments, which are the smaller the more numerous the fissures. The same thing would happen to the glacier if its thickness were less, and if the external heat had access to it on all sides. Nevertheless its surface decomposes more or less, the fissures dilate in consequence of the circulation, and the fragments are so dislocated as to be movable on one another without however becoming detached." —P. 163.

(12) "The angular fragments and the capillary fissures seem to disappear the moment the ice is covered. Thus on sweeping clean a part of a moraine, or the side of a gravel cone, the ice beneath is found to be perfectly smooth, and apparently without a trace of a fracture. But it is sufficient to leave these same surfaces uncovered for some instants, and the capillary fissures immediately show themselves, and, in consequence, the angular fragments. They appear with such regularity, that one might be tempted to believe that they are formed spontaneously at the very moment of their appearance. But on examining them with a little attention, one becomes convinced that they are of older date.

"I by no means pretend to deny that heat, acting suddenly at the moment the moraine is uncovered, may not develope some cracks. I have myself seen such cracks form suddenly (par éclat), but I conceive they are but few. If it were otherwise, and if the fissures were formed as they appear, it would be necessary to suppose that there are none in the ice of the moraine before it is uncovered, which would be contrary to all we know of the transformations of the ice."—P. 165.

(13) "Let us now make the opposite experiment, and cover with sand and gravel a portion of the surface of the glacier. However fissured and disaggregated it may be, the fissures and angular fragments will disappear at the end of some time so completely, that on removing the gravel the surface will be found as compact and transparent as that of a portion of moraine which has never been uncovered. And yet it is not probable that the fissures have reunited during the interval. It is, on the contrary, the gravel, which, intercepting the air and keeping the fissures full of water, renders them invisible, and gives to the whole mass a false appearance of compactness, which ceases the moment the air again has access to the fissures."—P. 166.

If the extract (8) were to be taken merely as a description of the superficial layer of a glacier, I should only have to object, that, so far as I have been able to observe, the colour of the disintegrated blue veins is not much affected by the water they contain, and that no amount of watery infiltration will confer on the white ice the beautiful transparency and colour of the blue veins. But Prof. Agassiz over and over again affirms that the whole substance of the glacier is traversed by capillary fissures, and his infiltration experiments are supposed by himself conclusively to demonstrate the fact. I must confess, however, that I have neither been able to observe what Prof. Agassiz supposes he has observed, nor, were our observations in unison, could I admit his explanations.

Take for instance the citation (9). How can the elasticity of the air-bubbles influence the formation of fissures in the continuous mass of rigid and eminently brittle ice which encloses them? How is the statement, that the ice becomes more rigid as the fissures are developed in it, these fissures being supposed to be filled with water, compatible with that made in (2), that this same water is the chief source of the plasticity and compressibility of ice?

Again, I am at a loss to understand the "diathermanicity" theory. Prof. Agassiz brings forward no experimental proof that air contained within ice is more heated by the sun's rays than the ice itself; and, *a priori*, it seems improbable that the more diathermanous body should be more heated than the less. It is true, I cannot pretend to have "followed the progress of modern physics;" but I am emboldened to say this much by the fact, that you, who have, seem to find at least equal difficulty in adopting Prof. Agassiz's explanation.

With regard to the experiments detailed in (10), (12), and (13), it will be observed that my results in the main agree with those of Prof. Agassiz, if, as before, we confine ourselves to the superficial layer; but, as I have shown, it is an error to extend the conclusions drawn from the structure of the superficial layer to the deep ice. This, however, is what Prof. Agassiz has done; and it is curious to find him in (12) refusing to follow out a suggestion which would have led to the solution of his difficulty, because it is "contrary to all we know of the transformations of the ice." What do we know at present of the transformations of the ice?

It is important to remark again, that *as regards matters of fact*, Prof. Agassiz's statements with respect even to the deep ice are, so far as they go, not essentially different from mine. He admits (12) that no fissures are at first visible in the deep ice;—had he taken the trouble to make the experiment, he would have found also that

coloured liquids cannot be made to enter it;—and he admits that the establishment of a complete system of fissures through a block of ice, and its consequent permeability, are matters of time and exposure (10). See also citation (1), and p. 289 of the 'Système Glaciaire.'

I omitted to make the experiment detailed in (13). It is singular that in (12) Prof. Agassiz states that "the angular fragments and the capillary fissures seem to disappear *the moment* the ice is covered," while in (13) the operation is said to take some time; but, supposing the fact to be as Prof. Agassiz says, it seems to me to be in the highest degree probable that the fissures *have* reunited during the interval. At any rate, I cannot admit Prof. Agassiz's explanation, for surely loose gravel is not exactly a substance calculated to "intercept air and keep fissures full of water."

It would take up too much space, and serve no useful purpose, to quote at length the account Prof. Agassiz gives of his infiltration experiments ('Syst. Glaciaire,' pp. 170–179). Those who will turn to the original, will find that they are all vitiated by the absence of any discrimination between the deep and the superficial ice, and between "capillary fissures" and accidental cracks. Not one of Prof. Agassiz's experiments affords the slightest evidence that capillary fissures are a primitive and essential constituent of the structure of the deep ice of a glacier.

The experiments of the Messrs. Schlagintweit (*l. c.* p. 12) appear to me to be equally inconclusive; these gentlemen, like Prof. Agassiz, having omitted to take the precaution of clearing away the superficial layer from the mouth of the cavity to be filled with the infiltration fluid. Unless this be done, the superficial layer sucks up the coloured liquid, which becomes diffused in the way they describe. And if the cavity (as may readily happen, especially with such large ones as those employed by these experimenters) communicates by an accidental fissure with some other part of the surface of the glacier (say the wall of a crevasse, or the roof of such a cavity as Prof. Agassiz's infiltration gallery), it should be well remembered that the fluid which drains through will not run out in a stream from the termination of a crack, unless the superficial layer has been cleared away; otherwise, it will fill the fissures of the superficial layer and appear as a great patch. The observer then, seeing nothing but fissures full of coloured infusion at each end of the course of the fluid, naturally enough imagines that in its intermediate course the fluid has traversed similar fissures. This conclusion would be at once dissipated by cutting away the superficial layer and laying open the

infiltration cavity,—a precaution which does not seem to have occurred to either Prof. Agassiz or the Messrs. Schlagintweit.

I will conclude with a few words upon the relation of structure to the arrangement of dirt upon the surface of a glacier. The great "dirt-bands" have never been *proved* to be connected with any peculiar structure of the ice on which they lie, and it has been shown that they *may* be the mere result of the influence of the motion of the glacier upon the form of any patch of dirt scattered accidentally upon its surface; but besides these "dirt-bands," the dirt on a glacier frequently presents a definite arrangement upon a smaller scale, which *is* connected with the minute structure of the glacier. We have both observed, for instance, in those parts of the Mer de Glace in which the structure is vertical, that the superficial layer of the wall of a crevasse is weathered into granules of tolerably even size and similar form. Nevertheless, dirt (or a coloured infusion) accumulates in larger proportion in those fissures which are parallel with the cleavage, and thus, from a little distance, the surface of the ice appears as if striated or ruled with lines parallel to the structure. The lines are separated by the width of the granules, and there may be several interposed between two blue veins.

Why it is that those intergranular fissures which are parallel with the cleavage are the larger, is a question I will not for the present attempt to answer. It may be that the weathering takes place more rapidly in this direction, or it may be that these fissures being in the course of the flow of the water produced by the superficial waste of the ice, become enlarged more rapidly than the others.

These markings, and the similar ones frequently to be observed on the upper surface of a glacier, might be termed "dirt-lines," to distinguish them from the great "dirt-bands." There is a third mode of arrangement of dirt, which, like the "dirt-lines," is dependent on the weathering of the ice, but the resulting striæ are broad streaks, and not mere lines. These may perhaps be termed "dirt-streaks."

I became acquainted with these quite recently, when, induced by Prof. Forbes's description and representation of the "structure" of the glacier of La Brenva, I paid a visit to that glacier. Prof. Forbes states,—

The alternation of bluish-green and greenish-white bands which compose this structure, gives to this glacier a most beautiful appearance as seen from the mule-road. An attempt has been made in plate 5 to give some idea of this most characteristic display, and which is better seen here than in any other glacier whatever with

which I am acquainted. The sketch was taken by myself from the point marked *k* on the map in July 1842."—*Travels*, 2nd Ed., p. 203.

It must at once strike any one conversant with the ordinary character of the veined structure, that at the distance of the point on the mule-road from which Prof. Forbes's view is taken any veins of the usual dimensions must be totally invisible; and I therefore approached La Brenva with the desire, if not the hope, of making the acquaintance of glacier structure on a new and gigantic scale.

Viewed from the mule-path, or from the old moraine at the commencement of the pine wood celebrated by De Saussure, the lower part of the glacier of La Brenva exhibits numerous crevasses, which appear to run nearly parallel with its length, so that the icy mass is divided into a series of parallel crests or ridges. The lateral faces of these ridges form perpendicular cliffs of ice, and present dark stripes directed in a longitudinal and nearly horizontal direction; but where an end view of a ridge is obtained, the stripes run either horizontally and transversely (as in the more central parts of the glacier), or are curved up towards the sides (as in the more lateral parts).

These markings are evidently those described and faithfully figured, as the "structure" of the glacier, by Prof. Forbes; but I cannot say I should have called them bluish-green. They looked to me simply dark and dirty. But I should state, that the weather, when I visited the glacier, was wet and cloudy.

Nevertheless, on descending on to the glacier itself, I found its structure, though very beautifully developed, to be in nowise remarkable for the size of its veins, which varied in length from an inch to eight or nine feet, and in breadth from a fraction of an inch to nine or ten inches. Veins of the latter dimensions, however, were rare; the majority having a thickness of less than an inch. The lenticular form was very well marked, and the veins were commonly separated by less than their thickness of white ice. I need hardly say that these veins became indistinguishable at a very short distance.

The streaks so conspicuous a long way off, on the other hand, became less sharply defined as I approached, and at length showed themselves to be nothing more than accumulations of the fine dirt—spread more or less over the whole cliff-like wall of ice,—in streaks of four to ten inches in breadth, and of variable length. They ran parallel with one another and with the structure, at a distance varying from a few inches to six or seven feet; and they were entirely superficial, the dirt never extending deeper than the weathered superficial layer.

It became clear, therefore, that the markings were neither structure nor stratification, but a peculiar kind of dirt-marks ; and the next point was to ascertain the conditions of their formation.

On close examination, the face of the ice-cliff exhibiting these markings appeared to be worn into a sort of wavy or rippled surface, the length of the ripples having a general direction downwards. The close-set veins, on the other hand, traverse the face of the ice, as has been said, nearly horizontally. The whole surface of the ice is more or less dirty, not half-a-dozen square inches being without its little grains of sand and minute gravel, brought down, as I imagine, by the water which continually trickles from above ; but the greater part of this impurity is invisible from a small distance, unless where it is specially accumulated.

Such accumulation takes place in two localities ; in the first place, on the little shelves afforded by the upper and more southerly aspects of the "ripples" above referred to. Here the dirt accumulates quite independently of the structure, and as a consequence either of the form or of the aspect of the part on which it lodges.

From a little distance these aggregations appear as spots and patches, but further off they cease to be visible, and the glacier between the horizontal streaks appears white.

These streaks mark the second locality in which the dirt aggregates. Now whenever I carefully examined the surface of the glacier at these points, I found it to be weathered into large granules, separated by coarse fissures which extended for a considerable depth into the substance of the glacier ; while the parts intermediate between the streaks, and which appear white from a distance, presented very much smaller granules, with fissures proportionately finer, and extending inwards for but a very small distance. In short, where the dark streaks existed, the ice was deeply weathered and coarsely granular, affording lodgment for dirt to a depth of two or three inches ; while the intermediate substance had undergone only superficial weathering, and its finely granular structure afforded but little facility for the intrusion of foreign matters.

The "dirt-streaks," then, are due to the unequal weathering of the ice ; but why does the ice weather unequally ? On seeking for an answer to this question, I found that every dirt-streak corresponded either with a very large blue vein, or with a closer aggregation than usual of smaller blue veins, while the intermediate substance contained a preponderance of the smallest blue veins ; so that the coarse granules were the result of the weathering of parts of the glacier, composed either exclusively, or for the most part, of blue ice, while those in

which the proportion of white ice was larger, weathered less deeply and into finer granules.

The markings of La Brenva, then, are neither ordinary dirt-bands nor direct expressions of structure, nor direct evidence of stratification, but they are produced by the more ready lodgment of dirt in some parts of the superficial layer of the glacier than in others, in consequence of the more coarse and deep weathering of these parts; which, again, is the result of the predominance of blue ice over white in these localities.

Why blue ice should predominate at intervals in the substance of this glacier,—whether the like alternation of structure holds good in glaciers generally,—and whether it has any relation to a primitive stratification, are problems of great interest and well worthy of investigation.

With regard to the second, I will merely express a belief that some such alternation of structure does obtain in glaciers generally; for the appearances presented by good sectional views of glaciers, such as that exposed on the north side of the Allalein, are so similar to those exhibited by La Brenva, that I cannot doubt the identity of their cause. I had been in the habit of regarding the appearances referred to as direct evidences of stratification; but if my supposition be correct they will merely be evidences of an alternation of structure which may or may not depend on stratification.

XLVII

ON CEPHALASPIS AND PTERASPIS

Geol. Soc. Quart. Journ., vol. xiv., 1858, *pp.* 267–280

[Plates XXXI. and XXXII.]

THE genus *Cephalaspis* (Agassiz) was originally established to include four species of Devonian fishes,—*C. Lyellii, C. rostratus, C. Lloydii*, and *C. Lewisii*; but the differences between the first and the last of these species were so great, that the founder of the genus himself suggested the probability of their future separation.

The two groups of species are said by Prof. Agassiz to be contrasted not only by their forms, but also by their minute structure. In regard to form, the cephalic disc of *Cephalaspis Lyellii* is stated to possess an almost semicircular anterior outline, while its postero-lateral angles are greatly prolonged backwards. The middle part of the occipital region, Prof. Agassiz adds, is cut off almost square (coupée presque carrément). As regards this last point, however, my own observations are at variance with his description.

Several specimens in the museum of this Society show that the middle of the occipital margin is not truncated, but is greatly produced backwards, the margins of the produced portion being concave. The same peculiarity is clearly distinguishable in the specimen of *C. Lyellii* now in the British Museum, and figured by M. Agassiz, pl. 1. *a.* 2: indeed the artist has faithfully depicted the real contour of the occipital margin in the figure cited. The well-known occipital spine is supported by this produced portion of the disk.

The discoid bodies, corresponding to all appearance with the cephalic disc of *C. Lyellii*, upon which alone the species *C. Lewisii* and *Lloydii* were established, differ widely from *C. Lyellii*, being oval in contour and not prolonged into postero-lateral cornua.

The structural differences observable in the disk of *C. Lyellii* on

the one hand, and of *C. Lewisii* and *Lloydii* on the other, are thus stated by Prof. Agassiz :—

"In *C. Lyellii* the head is covered with a pavement of polygonal plates, altogether similar to that which covers the head of *Ostracion*. Each plate is convex in the centre, and is marked by radiating grooves ending at the margin in denticulations, by which the scales interlock. These scales appear to be osseous and to have their external surface enamelled. At the circumference of the disk they become confounded together, and the enamel presents wrinkles parallel to the edge." Elsewhere these plates are said to be "true scales juxtaposed."

In the 'Recherches,' M. Agassiz describes "fibrous bones of the head" under the "scales," and he particularly mentions and figures the radiating direction of these "fibres;" but in the 'Monograph of the Old Red Sandstone Fishes' I find the following general remarks applied to the whole of the *Cephalaspidæ* :—

"It would appear from the condition of the specimens preserved, that all the cranial bones were only protecting plates, which covered a cartilaginous cranium similar to that of the Sturgeons; at least I have never been able to discover any cranial bones deprived of that characteristic granulation, which indicates that the plates were in direct relation with the integument. Therefore, I think there can be no doubt that all these granular plates rested by their inner and smooth surface on a cranial cartilage, such as is found in cartilaginous fishes and in the embryos of osseous fishes."—*Monog. Grès Rouge*, p. 3.

Nevertheless, in speaking of the genus *Cephalaspis*, a few pages further on, Prof. Agassiz states that he has nothing to add to his previous account of the genus; so that I am puzzled to know what view I ought to ascribe to him at present. We shall see by-and-by that the last quoted is the only one warranted by the facts of the case.

The disk of *Cephalaspis Lloydii* is said to consist of an external striated enamel, of a middle layer "composed of granules similar to those of the bones of Chondropterygious fishes," and of an internal layer made up of superimposed lamellæ. Prof. Agassiz considers that this structure "singularly recalls that of the test of the *Crustacea*."

Notwithstanding these, partly real and partly imaginary, differences between his different species of *Cephalaspis*, Prof. Agassiz found in *Cephalaspis rostratus* (a species which I have had no opportunity of observing) a form and structure of so transitional a character that he included them all under the same genus.

That so close an affinity obtains between all the species of *Cephalaspis* has, however, been disputed latterly by M. Rudolph Kner, who in 1847 published a memoir in Haidinger's 'Naturwissenschaftliche Abhandlungen' for the purpose of proving that *C. Lloydii* and *C. Lewisii* are not piscine remains at all, but that they are the internal shells of a Cephalopod allied to *Sepia*, for which he proposed the name of *Pteraspis*.

M. Kner's reasoning is based upon his examination of the structure of a fossil (evidently closely allied to *C. Lloydii*) from the Silurian rocks of Gallicia. The form of this fossil, says M. Kner, is very similar to that of *C. Lloydii*; but it is larger, having a length of about four inches by a width of two. It consists of three layers. The innermost is shining, bluish-green, enamel-like, and presents four or five distinct lamellæ. This layer forms one continuous surface marked in the centre by a longitudinal depression, smaller at one end than at the other, and by obscure radiating lines. The upper part of the conical depression is covered with minute pores or depressions, which are visible in the deeper as well as in the more superficial layers, but become evanescent in its lower part.

Between the layer of enamel and the prismatic layer which succeeds it, there lies a thin dull layer, in some places of a brownish colour. This is followed by an excessively delicate lamina of enamel which lies upon the prisms.

The layer of prisms is one line thick, and in section presents a number of more or less hexagonal disks. The enamel passes for a short distance between the prisms. Externally the prisms lie on a granular layer, to which the outermost very delicate "epidermic" lamina marked with parallel striæ succeeds.

M. Kner asserts (supporting the statement by the authority of Heckel) that in no known fish does any such epidermic or prismatic layer exist, and assuredly no such continuous internal enamel-layer, as in the fossil; and he then proceeds to compare the latter with the cuttle-bone.

M. Kner would hardly have published his views, had he subjected his sections to a more minute and careful microscopical examination. But, even apart from the characteristically piscine structure of these disks, very strong objections suggest themselves. In fact, to get at any sort of resemblance, M. Kner has to compare the outer layer of the fossil with the inner of the cuttle-bone, and *vice versa*; and even the superficial resemblance in the striation of the two bodies is anything but close.

In Dunker and Von Meyer's 'Palæontographica' (B. iv. H. 3. 1855)

Roemer gives an account of a fossil, which he refers to the *Sepiadæ*, under the name of *Palæoteuthis*. Whether this body is or is not a Cephalopod, is a point I will not enter upon here; but Roemer in referring to Kner's Memoir, expresses the opinion that the *Pteraspides* are *Crustacea*.

Mr. Salter and myself described two new species of *Cephalaspidæ* allied to *C. Lloydii* (Ag.), in a note[1] appended to a paper read before this Society by Mr. Banks, in December 1855. Without acceding to Kner's views respecting the zoological affinities of such Cephalaspids, we adopted his name. The facts to be detailed in the present paper will, I believe, fully justify this step; and I shall hereafter speak of *C. Lloydii* and its allies under the generic name of *Pteraspis*.

Professor Pander[2] has recently described two Silurian species of *Cephalaspis* (*C. verrucosus* and *C. Schrenckii*) both from Rootsikülle. The former somewhat resembles *C. ornatus* (Egerton), having a highly ornamented and tuberculated upper surface. In the broad tuberculated antero-dorsal plates, separated from the head by a suture, it foreshadows *Auchenaspis*, Eg. *C. Schrenckii* has hexagonal ornamented plates upon its disk.

Professor Pander appears to think that the margins of the disk represent jaws, being led to this conclusion, apparently, by their production into short quadrate serrations, which he regards as teeth. Sections of these "jaws" and "teeth," examined microscopically, exhibited "a homogeneous base, in which clear and dark cells of the most various forms—rounded, elongated, and angular, with fine radiating branches, lay scattered, and were frequently disposed in concentric layers, where a tubercle rose above the general surface. Although they have not the same regular form as ordinary bone-lacunæ (such as occur in *Pterichthys* and *Coccosteus*), yet they can hardly be called by any other name. The very thin narrow teeth, closely united with the margins of the jaws, and coalescent with them, have a porous basis, and shining broad, sharp upper and lateral edges. If both surfaces are carefully rubbed down, the basis is seen to consist for the most part of a homogeneous transparent mass, full of small dark cells, from which the very fine tubuli radiate in all directions, branch out, unite with the neighbouring ones, and by their many anastomoses form a most complex network. Towards the shining surface, as well as anteriorly and posteriorly—at least, certainly, towards one surface—the cells cease; the tubuli, winding irregularly in the base, take a straight course, and ascend apparently with an enlarged diameter,

1 'Quart. Journ. Geol. Soc.' vol. xii. p. 100.

2 'Monographie der fossilen Fische des Silurischen Systems,' 1856.

without convolutions and rarely branching, towards the external sharp angle." (*l. c.* p. 46.)

I am not aware of the existence of any other account of the minute structure of *Cephalaspis* and *Pteraspis* beyond these; and I will therefore now proceed to the immediate subject of this paper, which is, to describe that structure more fully and, I hope, more accurately than previous observers have done,—to compare *Pteraspis* and *Cephalaspis*, pointing out their real differences and resemblances,—and finally to consider the bearing of the structural facts upon the question of the zoological position of these ancient fishes.

Cephalaspis. (Pl. XIV. [XXXI.])

In but few of the specimens of *Cephalaspis Lyellii* which I have had the opportunity of observing, has the external surface of the cephalic shield been well exhibited, or preserved over any considerable surface. Where best shown it is somewhat uneven, and presents that curious apparent division into polygonal (usually hexagonal) areæ which has been described by Professor Agassiz. On examining the apparent sutures closely, however, they have not presented to my observation precisely the appearance figured in the pl. 1*b*. fig. 2. of the 'Recherches.' They appear rather as if short, delicate, reddish-brown lines had been ruled across the line of junction of the sides of the hexagons, for some way towards the centre of each hexagon; and these lines are so gently convergent as to seem nearly parallel. Neither do I remember to have met with such strongly marked central elevations as those represented in the figure cited.

The inner surface of the disk has presented itself well preserved in more than one specimen. It never exhibits any trace of the apparent sutures of the outer surface (compare Agassiz's 'Recherches,' pl. 1 *b*. fig. 3, where this fact is clearly shown), but appears whitish, enamel-like, and very smooth where it is not furrowed by certain shallow and narrow depressions which radiate from the region of the orbits and occiput towards the margin, before reaching which they repeatedly subdivide and anastomose. I do not doubt that these are the impressions of the vessels which ramified under the disk during life. Sometimes, by the elevation of the substance of the disk into a wall on each side of one of these depressions, the latter may become almost converted into a canal, so as to retain a portion of the matrix. This however is a rare occurrence.

When the concave inner surface of a disk and the convex cast of another specimen are compared, it is at once seen that the "radiating

fibres" of the one correspond with the grooves and furrows of the other. The surface of the cast is remarkably darker than the surrounding matrix, and might not unreasonably at first be supposed to be of a different nature. When the inner surface of the disk is carefully examined with a magnifying glass, a number of reddish-brown minute dots appear scattered irregularly over its surface. It will be seen immediately that these are the internal openings of vascular canals which enter the substance of the disk.

If a vertical section of the cephalic shield of *Cephalaspis Lyellii* is carried through the orbits and perpendicularly to the axis of the body, it will be seen that the disk is exceedingly thin, hardly anywhere attaining $\frac{1}{40}$th of an inch in thickness, except at the margins and the spine, which are thicker. At the lateral margin the thin lamella is bent abruptly and almost horizontally inwards for about a quarter of an inch. It then suddenly thins so much as to be little more than a flexible membrane, which in the specimen now under description is pressed up into close proximity with the dorsal part of the shield (fig. 4).

The thinness and fragility of the disk of *Cephalaspis* render it difficult to obtain good sections for microscopical examination. The best I have seen (Pl. XIV. [XXXI.] fig. 1.) is taken at an angle of about 45° to the longitudinal axis of the head, and intersects the occipital spine just beyond its origin. The section of the spine is in the best condition, and may be described first.

It is about $\frac{1}{40}$th of an inch thick in its thickest part, which corresponds with the median ridge of the spine, and presents three regions or layers, distinguishable from one another partly by their minute structure, and partly by the different mode of distribution of the vascular canals by which the tissue is permeated in each. The innermost or deep layer (*d*) is made up of superimposed lamellæ not more than $\frac{1}{200}$ th of an inch thick, each of which sometimes appeared to be still more finely laminated.

Interspersed among these, at greater or less distances, are numerous osseous lacunæ, whose long axes are parallel with the planes of the laminæ (fig. 3). The length of these lacunæ varies greatly, but may be taken at $\frac{1}{2000}$th of an inch on the average; some, however, are twice or three times this length, while others are much less. The transverse diameter is equally variable; but none that I measured exceeded $\frac{1}{3000}$th of an inch in this direction. The form of the lacunæ is very irregular in consequence of the long branching and anastomosing canaliculi which are given off not only from their ends but from their sides. In some parts the innermost layer appears

almost black when viewed by transmitted light, in consequence of the quantity of air retained in the multitudinous lacunæ and canaliculi.

Large vascular canals, measuring from $\frac{1}{200}$th to $\frac{1}{400}$th of an inch in diameter, whose inner opening corresponds with the brown spots on the inner surface, traverse the innermost layer very obliquely, in their course towards the middle layer (fig. 1, *e*). Their branches are few, and for the most part run parallel with the main trunk; but they give off a great multitude of minute canaliculi, which an astomose with those of the nearest lacunæ. Such of these canals as I have seen in section were oval, their long diameters being parallel with the planes of the lamellæ. In the specimen described the walls of the canals are lined with a reddish matter (like oxide of iron); and a similar substance obstructs many of the canaliculi.

The middle layer (*c*) is distinguished from the inner by the rarity or entire absence of the lacunæ, and by the indistinctness of the lamination as compared with that of the deep layer. Such striations of the nearly homogeneous base as seem to indicate lamination are, in the middle and inner parts of the middle layer, so disposed as to be nearly perpendicular to those of the deep layer, appearing to follow the course of the vascular canals.

The latter are continuous with the large vascular canals of the deep layer, but they are smaller and form a close network. Each of the large canals, on reaching the middle layer gives off several branches, which run nearly parallel with the surface (and therefore greatly inclined to the course of the great canals), and anastomose with those around, above, and below them. In this particular part of the disk, in fact, a large canal gives off as many as three tiers of these lateral branches, separated from one another by not much more than their own diameter, and all ramifying and anastomosing with one another. These lateral vascular canals have at first a diameter of about $\frac{1}{900}$th of an inch; but many of their anastomotic branches are much smaller.

Sooner or later all these branches appear to end in a close "superficial network," *b*, which lies in the boundary between the middle and the superficial layers. The latter or third layer of the disk (*a*) sometimes appears structureless, at others presents an obscure vertical striation, as if it were, like enamel, made up of minute fibres. The superficial vascular network sends into it a great number of minute short processes, which branch out abruptly at their ends, like a thorn-bush or a standard rose-tree, and end in excessively fine tubuli, like those of dentine. The tubuli appear empty and are much finer than the vascular processes, which are usually full of the dark red matter

before referred to. Hence, when the section is viewed by transmitted light, the vascular canals are very distinct, and appear to end abruptly in the deep half of the superficial layer, while the tubuli have the aspect of fine, clear, sparsely ramified lines, by no means so readily visible. In some cases they seem to open on the surface. This substance, it will be observed, corresponds very closely in structure with the "cosmine" of Professor Williamson. I have been unable to find any trace of a "ganoin" layer external to it.

The superficial layer does not form a continuous whole, but is seen in the section to be divided into masses of various length by interspaces or gaps, which extend as far as the superficial vascular network, the canals of which appear indeed to open into the bottom of the interspaces.

A structure in every essential respect similar to that just described is to be found in all other completely ossified parts of the cephalic shield, whether dorsal or ventral. In other regions of the dorsal part, however, the lamination of the inner layer is far more marked; and as a general rule the middle layer in these parts of the shield is thinner and contains fewer layers of lateral vascular ramuscules. The like is true of the inner part of the ventral region, in which only a single layer of close-set vascular canals makes its appearance (Pl. XIV. [XXXI.] fig. 5). The flexible part of the ventral layer appears to be composed of the lamellar inner layer only; and the thick margins of the disk resemble the spine in structure.

The structure of the ventral layer, enclosed as it is on both sides by the matrix, is usually very well displayed in sections, and the better, on account of the dark reddish-brown hue which is acquired by the matrix, for some little distance from its line of contact with the animal substance. But neither in these nor in any other sections can any trace of bony substance be discovered beyond that which enters into the composition of the thin cephalic shield itself. I believe, therefore, that the so-called "fibrous bone" is nothing but the surface of the matrix impressed by the inner surface of the disk, and stained of a darker colour than elsewhere.

If flakes of the inner layer of the shield be detached and well soaked in hot Canada balsam, they become transparent, and their structure is well displayed in a superficial view (fig. 3). At their broken edges, the lamellæ of which they are composed are seen cropping out one beyond the other; but their most striking feature consists in the long lines of lacunæ which lie in parallel and equidistant series in each layer, so that under a low power it appears to be composed of broad flat fibres arranged side by side. The axes of the lacunæ of each

layer are directed nearly at right angles to those of the layers above and below, so that under a low power the section appears cross-hatched by a series of dark lines. The great vascular canals are well seen traversing the successive lamellæ very obliquely.

In flakes of the disk similarly treated, but containing more of the middle and outer layers, fig. 2, it is obvious that the great canals divide into the branches of the middle layer which have already been seen in the vertical section, chiefly, if not only, along lines corresponding with the apparent sutures between the so-called "polygonal scales." The canals of the middle layer are very singularly arranged, passing from their origin, across these sutural lines and nearly parallel with one another, towards the centre of the adjacent "scales." The appearance of distinct "scales," and of the curious lines along their boundaries, is entirely due to this vascular distribution, the canals with their reddish lining showing very distinctly against the whitish general substance. In these views, again, the fissures by which the superficial layer is interrupted in the sectional view are seen to be nothing more than the expression of the valleys between the irregular and inconspicuous tubercles into which the superficial layer is raised (Pl. XIV. [XXXI.] fig. 2).

PTERASPIS. (Pl. XV. [XXXII.]).

A fragmentary specimen of *Pteraspis Banksii* (belonging to Mr. Marston) affords by far the best view I have yet met with of the general structure of the shield of this genus. A cast of the outer surface is exhibited, and for the greater part of its extent the substance of the shield is absent; but in the centre a patch is left, exhibiting all the layers in their natural condition and relations (fig. 2).

The innermost layer (*d*) is composed of a reddish-white nacreous substance, exhibiting a distinct appearance of lamination at its free edges: its surface is somewhat uneven, and presents scattered rounded apertures about $\frac{1}{400}$th of an inch in diameter. The edges of these apertures were not unfrequently somewhat raised; and their cavities were full of a reddish matter. External to the innermost layer is the middle layer (*c*), composed of vertical plates of a laminated substance of similar appearance to the inner layer, and varying in thickness from $\frac{1}{200}$th of an inch downwards. These plates are so disposed as to form a network, enclosing polygonal (4–5–6-sided) cells of an average diameter of about $\frac{1}{50}$th of an inch.

The inner apertures of these cells are closed by the inner layer. Externally, they are also closed by a substance of the same nature as their walls, but perforated by a variable number of apertures some-

what smaller than those in the inner layer (*b*). The inner surface of this substance presents in many cases a striation more or less parallel to the sides of these apertures; and when it is broken away the thickness of the layer which closes the outer apertures of the cells is seen to be permeated by numerous small canals which give it a sort of worm-eaten or reticulated appearance. I will call this the "reticular layer." Lastly, outside the reticular layer is a white substance, very imperfectly visible in this specimen, in which no canals are visible, and which constitutes the external layer (*a*).

A view, the precise complement of that just described, is afforded by another of Mr. Marston's specimens of *Pt. Banksii*. This exhibits, for the most part, a cast of the internal surface; but towards the edge a considerable portion of the shield is left in a very perfect state of preservation, and with its external surface intact. The external layer is produced into strong ridges, the summits of which are turned outwards and their bases juxtaposed. The summits of the ridges are as much as $\frac{1}{160}$th to $\frac{1}{170}$th of an inch apart. In some cases they were sharply angular, in others more rounded. Where this layer was broken away, the reticular layer beneath it, and the polygonal cells of the next layer were well displayed. The bottoms of these cells were seen to be closed by the inner layer, and in this apertures were visible, corresponding with those on its inner surface. I have not examined transverse sections of this species; but the structure of *Pt. Lloydii* is so similar, that its transverse section perfectly elucidates the appearances presented by *P. Banksii*.

I have seen no specimen exhibiting the unaltered external surface of *Pt. Lloydii*; but its internal surface and its other layers, where the inner one is broken away, are well displayed in two specimens belonging to the Geological Society. The inner layer is thin, whitish, and nacreous, and presents, scattered over its surface, apertures of a similar character and size to those shown by *Pt. Banksii*.

The next layer appears, at first, to be very different, inasmuch as it seems to be composed of irregular reddish prisms with white interspaces. The prisms have a diameter of $\frac{1}{80}$th of an inch, more or less.

The reticular layer is hardly distinguishable in this view; but when the apparently prismatic substance is broken away, either a thin filmy outer substance is visible, or a peculiar striation. A thin section of the shield of *Pt. Lloydii* (fig. 1), taken perpendicularly both to its plane and to its long axis, exhibits the following appearances when viewed with a low power by reflected light.

The total thickness of the section is about $\frac{1}{40}$th of an inch, and of this amount about $\frac{1}{110}$th of an inch is occupied by the inner layer,

$\frac{1}{140}$th of an inch by the second layer, $\frac{1}{300}$th of an inch by the next, and $\frac{1}{200}$th by the outermost layer.

The outer layer (*a*) appears to consist of a series of papillary elevations which have a broad free end, and are attached by narrow bases, so that a triangular interspace with its apex outwards is left between every pair of elevations. The matrix filling these interspaces, and for some distance in the immediate vicinity of the outer surface, is much darker than elsewhere, and has a deep brown hue. The attached ends of the elevations pass into a whitish substance, which, under this power, looks similar to their own. It is traversed by many reddish canals, which send diverticula into the elevations (*b*); and hence this substance clearly represents the "reticular layer" of *Pt. Banksii.* At intervals of about $\frac{1}{70}$th to $\frac{1}{110}$th of an inch or thereabouts, thin septiform processes are given off from the reticular layer, and pass perpendicularly inwards to the inner layer; they thus subdivide the second layer into a series of irregularly quadrate spaces, corresponding with the prisms seen in the superficial view.

The inner layer is, like the rest, whitish, and is traversed parallel with its surface by four or five much whiter streaks, so that it appears to be composed of only a corresponding number of lamellæ; but on allowing the light to pass through the section, it is at once obvious that each of these apparent lamellæ is in reality made up of many of the primitive laminæ which constitute the inner layer, and that the bright and dull white streaks are due entirely to a difference of texture or composition in the successive groups of laminæ.

Under a high power the laminæ are seen to have a thickness of about $\frac{1}{1300}$th of an inch, and to run nearly parallel with, and closely applied to, one another. They present an indistinct vertical striation, but exhibit no canals nor lacunæ. The septa of the second layer are composed of similar laminæ, but less distinct, and curved in various directions, usually more or less parallel to the walls of the large cavities which they bound. A fragment of the inner layer (fig. 4), rendered transparent by Canada balsam, and viewed by transmitted light, shows that it contains no lacunæ; nor have I been able to detect any distinct structure in its laminæ, unless an obscure and very delicate striation, visible here and there, may be regarded as such.

A similar disposition of curved laminæ can be traced in the "reticular layer;" but in the elevations of the external layer, such laminæ are no longer distinctly visible, although here and there traces of them may be seen. Each elevation, in fact, nearly resembles the tooth or dermal defence of a placoid fish. It contains a central cavity, commonly filled with a dark red matter, which usually occupies the

centre of the basal half of the elevation and then suddenly ends in a number of excessively minute branches, which pass towards the surface, ramifying as they go, and closely resembling the canals of dentine or cosmine. They appear to terminate on the surface, on which I have been unable to discover any trace of laminated structureless ganoin. The central canals of the elevations open internally into the network of vascular canals which lies in the reticular layer. These canals rarely exceed $\frac{1}{700}$th to $\frac{1}{800}$th of an inch in diameter, and they are rendered particularly obvious by the dark red granules with which their walls are dotted.

Internally they open directly into the interspaces of the septa which connect the reticular with the inner layer, and the granules are continued on to the walls of the septa, which are themselves occasionally traversed by short canals. The interspaces (*e*) are full of a more or less transparent inorganic matter, identical with that of the matrix. It follows, therefore, that the "bony prisms" or "granules which have been described have no existence, these so-called prisms being nothing but the matrix which has filled up the cavities of the polygonal cells, visible in their natural empty condition in *Pt. Banksii.* Canals resembling those of the reticular layer, as I have said, traverse some of the septa and put their chambers in communication.

In the section under description, the inner layer is for the most part devoid of canals; but one (*f*) is exhibited very beautifully. It has in the middle a diameter of about $\frac{1}{380}$th of an inch, but is wider at both ends, and traverses the inner layer almost perpendicularly. The laminæ are bent outwards for a certain distance, where they impinge upon its walls.

The structure just described is that of the central part of the section. At one of its ends, near the margin of the disk, the arrangement of the vascular channels is more like that in *Cephalaspis*,—the reticular layer assuming a much greater development, and the areolar character of the sinuses of the second layer becoming greatly obscured.

On comparing together the appearance of a section with those presented by the internal and external views of *Pteraspis*, there can be no doubt that the elevations of the outer layer of the one are the sections of the ridges of the other; and it is remarkable that there should be so striking a difference in the form of these ridges in *Pt. Banksii* and *Pt. Lloydii.* The ridges seen in concave casts probably always correspond with the whole interspaces between the ridges of the outer layer in *Pt. Banksii*; but it is quite conceivable that in *Pt. Lloydii* the ridges, in consequence of their peculiar form, might sometimes be held by the matrix and sometimes not; so that at one

time the ridges of the cast would be very narrow, corresponding only with the intervals between the summits of the ridges of the disk, sometimes broad, and corresponding with the intervals between their bases.

Comparison of PTERASPIS *and* CEPHALASPIS.

If the exposition which has just been given of the structure of *Cephalaspis* and *Pteraspis* be correct, it follows that neither the resemblances nor the differences in the structure of these two genera have hitherto been rightly apprehended.

The sole important differences consist, 1st, in the absence of osseous lacunæ in *Pteraspis*—their presence in *Cephalaspis*; 2nd, in the different general character and arrangement of the vascular sinuses; 3rd, in the different mode of arrangement of the external layer. These differences appear to me to be in themselves fully sufficient to warrant a generic distinction, but not more; for they are not greater than may be found among closely allied genera.

It will be observed that the account of the structure of *Pteraspis* given by M. Kner coincides, so far as it goes, with mine; and the examination of one of his *Pteraspides* (of which Sir Philip Egerton, with his usual liberality, has permitted me to have a section made), though not so satisfactory as I could have wished, still leads me to entertain no doubt that his fossils are really *Pteraspides*, and closely allied to *Pteraspis Lloydii.*

In this specimen, however, the histological characters which have been described are almost all undistinguishable. All that remains of the *Pteraspis* is a yellowish substance, without any definite structure, which appears in the section to form loops broader at their free than at their attached ends, and to send in longer or shorter reticulated processes of a similar character into the interior of the matrix. The interspaces of the loops are filled up with crystalline masses of carbonate of lime (?).

The length of the loop-like processes is about $\frac{1}{210}$th of an inch, and the breadth of their wide end about the same; the width of their necks is not more than $\frac{1}{330}$th, or thereabouts.

Now these are, as nearly as may be, the average dimensions of the sections of the ridges of *Pteraspis.*

No one can, I think, hesitate in placing *Pteraspis* among Fishes. So far from its structure having "no parallel among Fishes," it has absolutely no parallel in any other division of the animal kingdom. I have never seen any Molluscan or Crustacean structure with which

it could be for a moment confounded. Its relations with *Cephalaspis*, on the contrary, are very close. In each the shield is excessively thin, and composed of three or four layers :—1st, an "internal," composed of lamellæ parallel with the surface, and traversed more or less obliquely by vascular canals ; 2nd, next to this is a "middle layer," containing the network of wide canals or areolæ ; 3rd, the "reticular layer," described in *Cephalaspis* as part of No. 2, from which it is not distinctly marked in that genus ; 4th, the "external layer," consisting of a cosmine-like substance raised into ridges or tubercles.

The "bony granules," or "prisms," supposed to be characteristic of *Pteraspis*, the "polygonal ossicles" and the "fibrous bony layer," supposed to be peculiar features of *Cephalaspis*, have, as I have shown, no existence. Supposing that the shield of *Pteraspis*, like that of *Cephalaspis*, covered the animal's head (though there may be some ground for entertaining a doubt on this point), then it may be said that the presence of orbits in one, and their absence in the other, indicates a wide difference between the two genera. It must be remembered, however, that there is precisely the same difference between *Pterichthys* and *Coccosteus*, which are admitted by all to be closely allied.

Though I have had no opportunity of examining the Russian species, I believe I do not err in regarding what Pander describes as the teeth of *Cephalaspis* as merely an excessive development of the marginal tubercles of the outer layer. It does not appear to me that there is any evidence that the mouth was situated at the margin of the shield ; on the contrary, the inward prolongation of the reflected ventral layer leads me to suspect that the under surface of the head of *Cephalaspis* resembled that of *Loricaria* or of *Acipenser*.

Zoological position of CEPHALASPIS *and* PTERASPIS.

Leaving for the present Professor Pander's "Conodonts" out of view, *Cephalaspis* and *Pteraspis* are among the oldest, if they are not the very oldest, of known fishes ; and it is therefore highly interesting to inquire into their position in the scale of ichthyic nature.

Palæontologists in general, following Agassiz, classify them as "Ganoids ;" but it is to be feared that few persons who have not paid special attention to recent Ichthyology and to Comparative Anatomy have a clear conception of what is meant by the term "Ganoid."

The founder of the Order, allowing himself to attach an undue weight to mere secondary characters, included under the head of

"Ganoidei" a heterogeneous assemblage of Fishes characterized by very few common characters, save their hard and shining scales, and the abdominal position of their ventral fins, but embracing the Siluroids, the Gymnodonts, and the Ostracionts, while the genus *Amia* was allowed to remain among the *Clupeidæ.*

If these are all Ganoids, and if such are the characters of the Order, then doubtless *Pteraspis* and *Cephalaspis* are Ganoids.

Since the publication of the admirable and philosophical researches of Johannes Müller, however, the term *Ganoidei* has been received in a very different sense by the great mass of naturalists. Müller showed that the great majority of the recent Fishes classed as Ganoid by Agassiz, viz. the Siluroids, the Gymnodonts, the Ostracionts, &c., were in no essential respect different from the *Teleostei*, or true bony fishes, while the true recent Ganoids formed a small but extremely remarkable assemblage, characterized by a structure in many respects intermediate between that of *Teleostei* and that of the *Elasmobranchii* (or what are commonly called cartilaginous fishes). Müller showed, furthermore, that the character of the surface and the histological texture of the scales are of little systematic value, and reduced the diagnostic marks of a Ganoid, visible in the external skeleton, to two —the presence of "fulcra" and the articulation of the scales by gomphosis. The rest of the essential characters of the Ganoids are entirely derived from the soft parts—the brain, the heart, the branchiæ, and the air-bladder. A Ganoid is in fact distinguished from any other fish by the following peculiarities.

The optic nerves form a chiasma ; the bulbus aortæ is rhythmically contractile, and provided with several series of valves ; the branchiæ are free ; there is an air-bladder connected by an open duct with the intestine ; the ventral fins are abdominal. These essential characters are shared by only six genera of existing fishes—*Lepidosteus*, *Polypterus*, *Amia*, *Acipenser*, *Scapirhynchus*, and *Spatularia*—which are no less singular in their distribution than in their anatomy. All are essentially freshwater fishes ; all are found in the northern hemisphere ; three—*Lepidosteus*, *Amia*, and *Spatularia*—are exclusively North American ; *Polypterus* is only known in the Nile, while *Acipenser* is common to Europe, Asia, and North America.

Now what evidence have we that either *Cephalaspis* or *Pteraspis* are in the proper sense Ganoids ? There is nothing about their dermal covering peculiarly characteristic of Ganoids ; and as to the rudimentary state of ossification of the vertebral column, there are Teleostean fishes (e.g. *Helmichthys*) quite as imperfect in this respect as any Ganoid.

Without doubt there is a singularly close resemblance, in the structure of the dermal plates, between *Cephalaspis* and *Megalichthys* —the last being very probably a true Ganoid ; but the point of difference is noteworthy : *it is precisely the characteristic ganoin-layer which is absent in Cephalaspis.*

On the other hand, the arrangement of the hard tissues in *Pteraspis* reminds one almost as strongly of *Ostracion*, an undoubted Teleostean.

The existing fishes to which *Cephalaspis* presents the nearest resemblance in form, viz. *Loricaria* and *Callichthys*, are Siluroid Teleosteans, and not Ganoids ; and, if we take the immediate allies of *Cephalaspis* and *Pteraspis*, viz. *Coccosteus* and *Pterichthys*, their analogies with Siluroids, such as *Bagrus* and *Doras*, are as strong as those with *Acipenser*.

A careful consideration of the facts, then, seems to me to prove only the necessity of suspending one's judgment. That *Cephalaspis* and *Pteraspis* are either Ganoids or Teleosteans appears certain ; but to which of these orders they belong, there is no evidence to show.

If this conclusion is valid, it is clear that the ordinary assumption, that the earliest fishes belonged to low types of organization, falls to the ground, whatever may be the relative estimation in which the different orders of fishes are held.

But it is said that the great development of the dermal skeleton, combined with the rudimentary condition of the endo-skeleton, shows that these early fishes occupied a low place within their own group.

Mere *a-priori* argumentation on such questions as these would be a waste of time ; but, happily, we can put the principle involved in this reasoning to the test by direct observation. This principle clearly is, that the development of the exo- and endo-skeletons stands in some ratio to the general perfection of the organization of a fish.

Now the existing genera of Ganoids are, as I have said above, characterized by certain anatomical peculiarities common to all ; and, in every essential of organization, no one can be said to be superior or inferior to another. The same kind of brain, heart, and respiratory organs are to be found in all ; nevertheless, Nature seems to have amused herself with working out in this small group every possible variety and combination of endo-skeleton and exo-skeleton.

Lepidosteus has a greatly developed exo-skeleton, and the most Salamandroid vertebra known among fishes.

Polypterus has an equally well-developed exo-skeleton, and a well-ossified but piscine vertebral column.

Amia has scales as thin and flexible as those of a carp, with a well-ossified skeleton like that of an ordinary Teleostean fish.

Acipenser and *Scapirhynchus* have large enamelled dermal plates, constituting a well-developed exo-skeleton, with a cartilaginous vertebral column and persistent chorda dorsalis;

While, finally, *Spatularia*, with its mainly cartilaginous endoskeleton, has a smooth skin, without dermal plates at all.

In the face of these plain anatomical facts, what is the value of the argument from the development or non-development of the skeleton to the grade of organization of a fish?

EXPLANATION OF THE PLATES.

Plate XIV. [XXXI.].

Cephalaspis.

Fig. 1. Vertical section of the shield of *Cephalaspis*, magnified 100 diameters. *a.* Outer layer. *b.* Reticular layer. *c*, *d.* Middle and innermost substance. *e.* Vascular canals. *f.* Matrix.

Fig. 2. Horizontal section of the same, viewed from the outer side, showing the peculiar arrangement of the vascular canals along the so-called "sutures," magnified 50 diameters.

Fig. 3. Thin scale of the inner substance showing the osseous lacunæ of two laminæ, magnified 200 diameters.

Fig. 4. Outline of a vertical section through the shield of *Cephalaspis*, showing its inflected margin (*a*) and inferior flexible wall (*b*), magnified 2 diameters.

Fig. 5. Section of the inferior wall at the point of transition of the ordinary substance of the shield (*a*) into the thin flexible under layer (*b*), magnified 100 diameters.

Plate XV. [XXXII.].

Pteraspis.

Fig. 1. Vertical section, magnified 100 diameters. *a.* "Enamel"-ridges forming the outer layer. *b.* Reticular layer. *c*, *d.* Middle and inner substance. *e.* Cavity filled with matrix—one of the supposed "ossicles." *f.* Vascular canal. *g.* Matrix.

Fig. 2. Portion of the shield of *Pteraspis Banksii*, viewed from within: letters as in fig. 1: magnified 10 diameters.

Fig. 3. Vertical section of inner layer of *Pteraspis*, showing the laminæ and one of the vascular canals, magnified 100 diameters.

Fig. 4. A flake of the inner layer viewed from within, magnified 25 diameters. *a.* Vascular canals.

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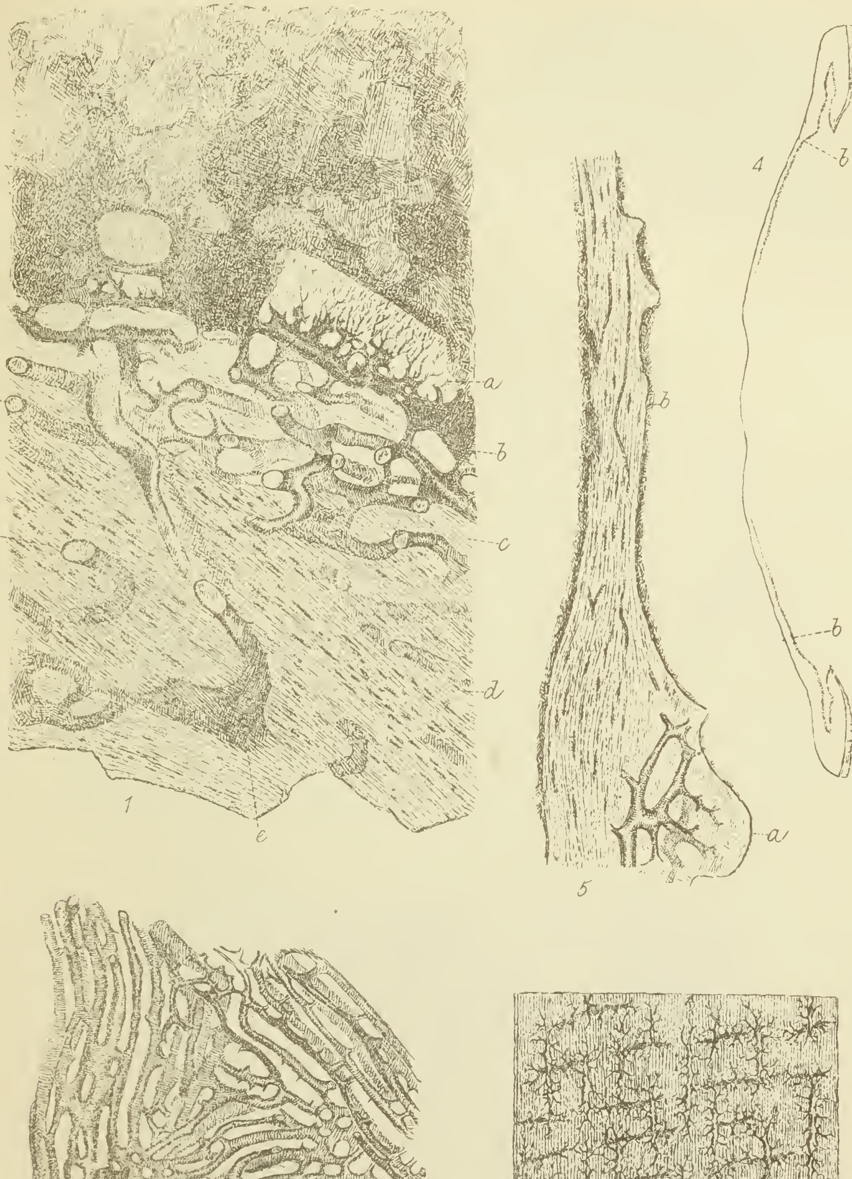
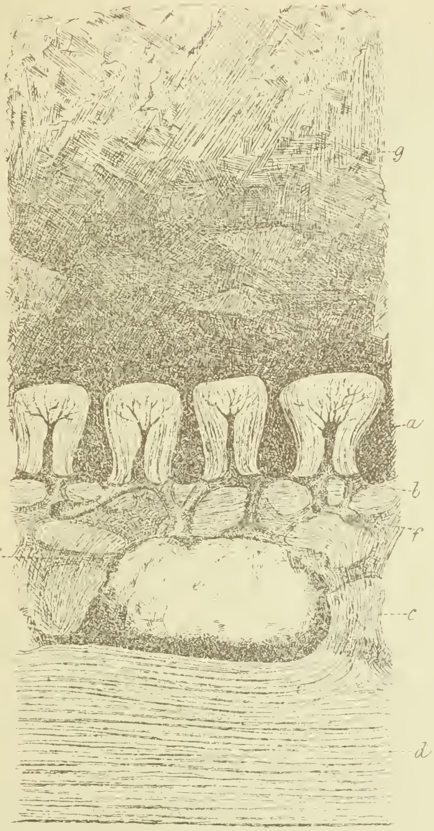


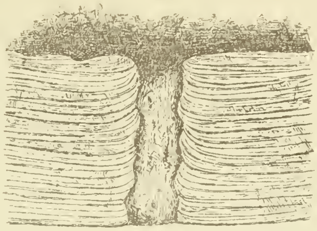
CEPHALASPIS

[PLATE XXXII]

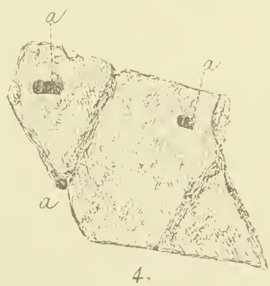
Quart Journ Geol Soc Vol XIV Pl XV.



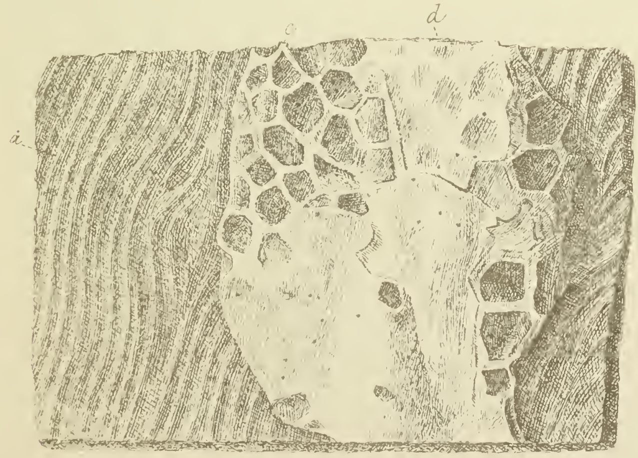
1



3



4.



2

PTERASPIS

XLVIII

OBSERVATIONS ON THE GENUS PTERASPIS.

Brit. Assoc., Rep. 1858 (*part* 2), *pp.* 82–83.

In a paper "On *Cephalaspis* and *Pteraspis*," recently read before the Geological Society, and published in the 'Quarterly Journal' for the present year, I endeavoured to prove,—

1st. That the *Cephalaspis Lloydii* and *Lewisii* of the author of the 'Recherches sur les Poissons Fossiles,' subsequently united into a distinct genus, *Pteraspis* (Kner), were rightly judged by Prof. Agassiz to be the remains of fish, and that they are not, as had been imagined by other naturalists, either Crustacean or Molluscan.

2nd. That, as Prof. Agassiz had surmised, they are at once allied to *Cephalaspis*, and generically distinct from it.

I grounded these conclusions almost wholly on histological evidence, or that afforded by the microscopic structure of the bodies in question. Not having seen the *Cephalaspis rostratus* of Agassiz, I abstained from offering any opinion with regard to it.

Since the publication of my paper a great deal of new material has passed into my hands, chiefly by the kindness of the zealous geologists and palæontologists who reside in and about Ludlow. Messrs. Cocking, Crouch, Harley, Lightbody, Marston, and Salwey, and I have thereby been enabled greatly to extend and confirm my conclusions with regard to the nature and affinities of these remarkable extinct fishes. A brief note of the results at which I have now arrived will perhaps be interesting to the Section.

The oblong plates which have hitherto been the only discovered parts of *Pteraspis* form only a portion of the great shield which covered

the anterior part of the dorsal region of the body. Apparently anchylosed or continuous with the anterior edges of some specimens of these plates, there is a bony disk, prolonged at its postero-lateral angles into two long cornua, which pass into the edges of the oblong plate. The disk exhibits the characteristic structure and the peculiar striated sculpture ; it is prolonged anteriorly into a sort of rostrum, whose length varies with the species of *Pteraspis* : laterally it exhibits two well-marked nearly circular marginal apertures, which I make no doubt are the orbits.

I conceive, therefore, that the part in question corresponds with the anterior part of the cephalic disk of *Cephalaspis*, and that the oblong plate, which may well be termed the occipito-nuchal plate, answers partly to the posterior moiety of the cephalic disk of *Cephalaspis*, partly to that median backward prolongation of the posterior margin of the cephalic disk of *Cephalaspis* to which I have particularly directed attention in my memoir. It is from this that the strong nuchal spine of the *Cephalaspis* arises ; and as if to render the resemblance complete, the most perfect specimens of *Pteraspis* show that it had a like spine developed in a similar position.

There exists, indeed, a most interesting gradational series of forms between *Cephalaspis Lyellii* and *Pteraspis.*

The *Auchenaspis* of Sir Philip Egerton has a cephalic disk with the semicircular anterior outline of that of *Ceph. Lyellii*, but the interspace between the cornua of the disk is nearly filled up by the large nuchal plate, whose backward extent may have been greater than is exhibited by any of the specimens of *Auchenaspis* yet obtained. Enlarge the nuchal plate of *Auchenaspis* and give the cephalic disk a more produced anterior outline, and the result is the form of *Pteraspis.*

Throughout all these gradations of form, however, it must be borne in mind that the minute structure of the parts is such as at once to enable the observer to distinguish *Cephalaspis* from *Pteraspis.*

I ventured in my paper, read before the Geological Society, to say that the Ganoid nature of *Cephalaspis* and *Pteraspis* appeared to me to be unproved, and to allude to the relations between these genera and the great group of existing *Siluroidei.* Without at all wishing to push too far resemblances which, when we come to know more, may turn out to be mere analogies, I must say that the new facts which I have brought forward appear to point somewhat in the same direction. The siluroid fishes, in fact, are especially characterized by

the large bony nuchal plate which supports the great dorsal spine, and is constantly anchylosed to the posterior margin of the skull. The rostrum of the *Pteraspis* is not without its analogue in *Loricaria*.

On the other hand, that rostrum might be compared with the prolonged snout of *Acipenser*; and the shield of *Pteraspis* presents many points of similarity with the cephalic buckler of such fishes as *Dipterus*, *Diplopterus*, and *Osteolepis*.

XLIX

ON A NEW SPECIES OF PLESIOSAURUS FROM STREET, NEAR GLASTONBURY; WITH REMARKS ON THE STRUCTURE OF THE ATLAS AND AXIS VERTEBRÆ, AND OF THE CRANIUM, IN THAT GENUS.

Quart. Journ. Geol. Soc., vol. xiv., 1858, *pp.* 281-294.

THE locality where the *Plesiosaurus*, which forms the subject of the present brief notice,[1] was obtained is already famous for its richness in such remains. In fact, the limestone beds of the Lower Lias at Street have already yielded at least three species of *Plesiosaurus*—*P. Hawkinsii*, *P. macrocephalus*, and *P. megacephalus*; and it seemed so unlikely that a fourth species should have inhabited the same area, that I was for a long while unwilling to admit the distinctness of the form at present under consideration.

The evidence which I shall bring forward, however, seems to me to admit of no other conclusion.

The specimen is a remarkably fine one. The limestone matrix in which it is imbedded being hard and free from pyrites, every part is well preserved; and the value of the fossil is further enhanced by two circumstances:—first, the very slight amount of disturbance which the bones have undergone, so that the vertebræ from the third cervical to the last caudal are all in their natural positions; secondly, the perfectly lateral view of the body which is presented. The only important defects are the absence of the paddles, and the flattening and apparent loss of the lower jaw which the head has suffered.

The total length of the skeleton is about 7½ feet. The left side

[1] The specimen will be fully described and figured in the Decades of the Geological Survey of Great Britain.

is exposed, and the neck and tail are strongly bent upwards, as if the creature had died in a state of opisthotonic rigidity. The head is twisted, so that its upper surface only is visible, and it is at the same time bent back, at right angles to the neck. In consequence of this, the occipital condyle and the atlas are well separated. The two anterior cervical vertebræ were originally partially covered by the crushed right os quadratum; but by removing the latter both atlas and axis have been very clearly exposed.

As the Museum of Practical Geology is indebted to the judgment and energy of my friend and colleague Mr. Robert Etheridge, F.G.S., for the acquisition of this fine *Plesiosaurus*, I think I cannot do better than name it after him, *P. Etheridgii.*

The following are the most important characters of this species :—

1. The length of the skull (measured from the end of the premaxillaries to the occipital condyle[1]) is less than one-thirteenth of the whole length of the body. As the anterior teeth have nearly disappeared, it is not certain that the skull may not have borne a slightly larger proportion to the body; but the anterior slope of the premaxillaries clearly shows that the allowance to be made on this ground, if any, must be very small.

2. There are thirty cervical vertebræ—vertebræ, that is, which present facets for articulation with ribs on the lower half of their centrum; the ribs being short and compressed superiorly, or hatchet-shaped.[2]

3. Three times the length of the skull equals the length of the anterior twenty-three cervical vertebræ; four times the same length equals the anterior twenty-eight cervical vertebræ. It follows therefore that the neck is between four and five times as long as the skull.

4. There are about 90 vertebræ, of which 30 are cervical, 23 dorsal, 2 sacral, and 34 or 35 caudal.

5. The humerus and the femur are as nearly as may be equal in size.

6. The vertical diameter of the centra of the anterior cervical vertebræ is greater than the longitudinal, the proportion being at least as three to two in the third cervical. In the thirtieth cervical the two

[1] The "length of the head" measured from the end of the snout to the posterior extremity of the lower jaw is commonly taken as the unit of comparison. But the end of the os quadratum and the lower jaw are so readily displaced as to render this anything but a safe standard.

[2] The neurapophysial sutures are not visible; but as there is reason to believe that the neurapophyses do not extend upon the bodies of the cervical vertebræ beyond their dorsal half, the character of a cervical vertebra here used is probably equivalent to that employed by Prof. Owen (*loc. cit.*).

measurements are nearly equal, though the vertical predominates a little. So far as they are visible in the transverse sections exposed by fracture of the limestone slab, the articular faces of the centra are nearly circular.

7. The cervical costal pits are elliptical, about half as long vertically as longitudinally, and from the third to the twenty-sixth inclusive are divided lengthwise by a well-marked longitudinal depression; but there is no subdivision into two distinct facets. In all these vertebræ the pits look outwards and a little downwards, their axes are parallel with those of the vertebræ, and they are completely sessile.

In the last three cervical vertebræ the costal pits are directed more and more backwards as well as outwards, and take the form of flattened facets. At the same time their anterior edges are raised up by an outgrowth of the body of the vertebra.

8. The articular facets of the anterior dorsal vertebræ are nearly circular. In the anterior eight or nine dorsal vertebræ the transverse processes arise partially from below the level of the upper margin of the centrum. In the tenth they appear to arise completely above it, their upper margins being on a level with the upper edges of the posterior zygapophyses. In the eighteenth they begin again to descend, so that in the first sacral more than half the root of the transverse process is below the level of the superior margin of the body.

9. The neural spines of the cervical vertebræ are inclined a little backwards, and have their anterior edges bevelled, so that their apices are more or less pointed. Those of the dorsal and sacral vertebræ are vertical, with their anterior and posterior margins parallel and their apices squarely truncated.

10. The articular faces of the caudal vertebræ are nearly round, and their centra larger vertically than longitudinally. The neural spines slope backwards a little, but their anterior edges are straight and their ends truncated. The three or four last caudals have apparently neither spines nor neurapophyses.

There are more than thirty named species of *Plesiosaurus*. Of these, however, far more than half are founded upon detached bones, and I am not aware that entire, or nearly entire, specimens of more than four species, viz. *dolichodeirus*, *Hawkinsii*, *macrocephalus*, and *brachycephalus*, have as yet been described. This point is worthy of notice when we consider that the proportion of the head to the body constitutes an important datum in the determination of the species of this genus. I will compare *P. Etheridgii* first with those of which complete or nearly complete skeletons have been observed.

In *P. brachycephalus*, according to Prof. Owen, the head equals one-eighth of the body in length ; in *P. macrocephalus* the length of the head equals one-half that of the neck ; they are therefore at once excluded.

The classical authority on *Plesiosauri*, Mr. Conybeare, states that the head of *P. dolichodeirus* equals one-thirteenth of the entire body, or one-fifth of the neck, while the head and neck together are to the body as six to seven.[1] These proportions approach those of *P. Etheridgii.* But they are not the same ; and besides, the neural spines of the cervical vertebræ of *P. dolichodeirus* are quite differently shaped from those of *P. Etheridgii.* And though the total number of vertebræ in *P. dolichodeirus* is the same, viz. 90, 35 are said to be cervical, 27 dorsal, 2 sacral, and 26 caudal. Clearly then the specimen described has nothing to do with *dolichodeirus.*

Plesiosaurus Hawkinsii approaches it much more closely in size, form, and general proportions.

Several magnificent specimens of this species are to be seen at the British Museum, and afford excellent materials for the determination of its distinctive characters. Nevertheless the account of its characters in the 'Report,' already cited, presents some difficulties to the reader. At page 57, for instance, it is stated that in this species "the neck equals three lengths of the head, and the neck and head together equal the trunk and tail." If this be true, of course the length of the head must equal one-eighth of that of the whole body. Nevertheless, at page 61 of the same 'Report,' it is said that the head equals less than one-tenth part of the body.

Again, at page 61 (and by implication at page 63 ?), *P. Hawkinsii* is said to possess twenty-nine cervical vertebræ ; but at page 57 the number given is thirty-one ;[2] and thirty-one is stated to be the number

[1] In his well-known memoir (Geol. Trans. ii. 1, 1824) Mr. Conybeare states at page 382, "the neck is fully equal in length to the body and tail united ;" but at page 385 he says, "taking the head as 1, the neck will be 5, the body as 4, and the tail as 3 : the total length being, as before remarked, 13 times that of the head." Prof. Owen, in his 'Report on the British Fossil Reptilia,' quotes Mr. Conybeare's first statement, but omits to refer to the last. Prof. Owen further states (Report, p. 61) that in *Pl. dolichodeirus* the head is four times the length of the neck. I suppose this to be a misprint, and that what is meant is, that the neck is four times the length of the head ; but even this is at direct variance with Mr. Conybeare's assertions and figures.

[2] At least, this is the only conclusion consistent with the definition of a cervical vertebra at page 58. Prof. Owen there proposes to consider as *cervical* those vertebræ whose centrum exhibits the whole or a part of the costal articular surface. At page 57 he states with respect to *P. Hawkinsii*, "In the first or anterior 31 vertebræ the centrum supports the whole or part of the costal pit." Therefore, according to the definition, these 31 vertebræ are cervical.

in this species in the same author's memoir on *P. macrocephalus* (p. 523). No less contradictory are the statements as to the number of dorsal vertebræ. At pages 57 and 58 of the 'Report' they are by implication estimated at twenty-five; but at page 66 they are said to be twenty-three. I can nowhere find the slightest indication that Prof. Owen imagines the number of cervical or dorsal vertebræ to be variable in the same species of *Plesiosaurus*. The opposed statements which I have quoted are wholly devoid of the comment which would have been naturally evoked by the discovery of so remarkable a fact.

The specimens of *Plesiosaurus Hawkinsii*, on which the description of the species, contained in the 'Report on Britist Fossil Reptilia,' is chiefly based, are, I believe, those now contained in the Collection of the British Museum. Of these specimens three, viz. that numbered $\frac{2000}{18}$ and figured by Mr. Hawkins in his plate 24, that numbered 14,549 and figured in plate 28 of the same work, that numbered 14,541 and figured in Hawkins's plate 27, are but little disturbed, and retain the head and neck *in situ*.

In a fourth specimen, 14,550, which is in many respects extremely valuable and instructive, the head is unfortunately displaced and the anterior cervical vertebræ are absent.

Besides these four specimens, there is a fifth *Plesiosaurus*, numbered 2000 and named *dolichodeirus*; it is however certainly either *Hawkinsii* or *Etheridgii*, and I believe the latter, although the absence of the head and anterior cervical vertebræ renders it hazardous to give a confident opinion.

I will speak of these specimens in the order here named, under the heads of Nos. 1, 2, 3, 4, and 5. But I must first remark, that no one of them affords the means of determining the number of the dorsal vertebræ with so much certainty as in *P. Etheridgii*. To ascertain the number of the dorsal, or dorso-lumbar, vertebræ in any vertebral column, it is obviously necessary that we should be able to assure ourselves of these facts:—1st, that we know which is the last cervical; 2nd, that we know the first sacral; and 3rd, that we know how many vertebræ intervene between these.

In No. 1 the vertebral column is so obscured by the ribs and pectoral and pelvic girdles, that no one of these points can be ascertained with accuracy. In No. 2 the anterior part of the sixth vertebra from the skull is gone, and it is impossible to be certain that a whole vertebra may not have disappeared; at the same time an uncertain number of vertebræ have been displaced from the middle region of the back.

In No. 3 the dorso-sacral vertebræ are hidden in the same way as in No. 1.

In No. 4 the head and anterior cervical vertebræ are removed, and the dorsal region is dislocated, the hinder part of the vertebral column overlapping the anterior.

No. 5 alone exhibits the posterior part of the cervical and the whole dorsal region undisturbed. Either the sixteenth or the seventeenth vertebra in the series, counting from the first (broken) one, is here certainly the first dorsal—I believe the seventeenth.

The forty-second vertebra is certainly caudal; hence as there are two sacrals, $42-(17+2)=23$, which is the number of dorsals in *P. Etheridgii*, to which this specimen has in other respects a close resemblance.

Under these circumstances I can only suppose that Prof. Owen has some other evidence than that mentioned in his 'Report' for the following statement:—

"From the 32nd to the 56th vertebra inclusive, the costal articular surface is wholly impressed on the neurapophysis."—(Report, p. 57.)

Now, as Prof. Owen states in his memoir on *P. macrocephalus* (p. 527), that in the sacral vertebræ of *P. Hawkinsii* "a small part of the costal articular surface is contributed by the centrum," it necessarily follows that these twenty-five vertebræ (32nd to 56th inclusive) are neither sacral nor cervical, but dorsal. It is true that at page 66 of the 'Report' Prof. Owen affirms that there are only twenty-three dorsal vertebræ; but I cannot venture to set this cursory contradiction against a definite anatomical statement like the foregoing.

I have been most desirous to arrive at a clear understanding of Prof. Owen's definition of the species *P. Hawkinsii*; but after long and careful study I can only arrive at the following alternatives:—

Either 1. The apparently contradictory statements which I have quoted have been made through the use of a double definition of a "cervical vertebra,"—meaning thereby in one case a vertebra with a certain kind of rib, in the other a vertebra with a certain kind of costal articular facet;—

Or 2. Believing the number of cervico-dorsal vertebræ to be constant in the same species, Prof. Owen conceives that the special dorsal modification may commence either at the 30th or at the 32nd vertebra, according to individual variations.

On this hypothesis it must be assumed that the smaller number of dorsal vertebræ assigned to this species was found in that individual which exhibited the larger number of cervicals, and *vice versa*. The

numbers in the one case would be $31+23=54$, in the other $29+25=54$.

Or 3. Prof. Owen imagines that the total number of cervico-dorsal vertebræ may vary between 52 $(29+23)$ and 56 $(31+25)$ in different individuals of the same species.

I am not aware that a shadow of evidence exists in favour of the occurrence of so remarkable a variation as the last-named in any vertebrate animal so highly organized as the *Plesiosaurus*. If the second be the right interpretation of Prof. Owen's views, then *P. Hawkinsii* will always have the same number of cervico-dorsal vertebræ, and that number is according to Prof. Owen at least fifty-four, and at most fifty-six. I have shown, however, that in *P. Etheridgii* there are only fifty-three cervico-dorsal vertebræ.

I beg to repeat, however, that I can find no proof of the existence of fifty-four cervico-dorsal vertebræ in any *P. Hawkinsii* in the British Museum. Under these circumstances it became necessary to inquire whether the proportions of the head, body, and neck might not furnish the needful marks of specific distinction. Measuring these in the same way as *P. Etheridgii*, I find with regard to No. 1 that—

1. Taking the length of the skull (from the occipital condyle to the end of the snout) as 1, the whole body measures between 10 and 11. Taking the head from the end of the snout to the end of the lower jaw as 1, the whole body measures between 8 and 9.

2. Three times the length of the skull equals the anterior 25 vertebræ; four times the same length equals the anterior 31 vertebræ.

In No. 2 the end of the tail is gone, and therefore the proportions of the skull to the entire body cannot be ascertained; but three times the length of the skull measured along the neck reaches the middle of the twenty-fifth cervical vertebra, and four times equals the 31 vertebræ as before.

In No. 3 the length of the skull is rather less than one-eleventh of the whole body; while the length from the snout to the angle of the jaw is rather less than one-ninth of the whole body. The proportions of the head to the neck are as in No. 1.

In No. 1 the rib of the 29th cervical vertebra is hatchet-shaped; the shape of the ribs of the 30th and 31st vertebræ is not certainly discoverable, nor can the character of their articular surfaces be clearly made out.

In No. 3 the rib of the 29th vertebra is truly hatchet-shaped. Those of the 31st vertebra cannot be made out clearly, nor can that of the 30th on the left-hand side. On the right side the head of a rib lies against the posterior part of the neural arch of this vertebra;

and, though its produced angle is more or less broken, its hatchet-shape can be clearly distinguished. The costal articular facets of both the 30th and 31st vertebræ are traversed by the neurapophysial suture.

In No. 2 the condition of the posterior cervical vertebræ is such as to render it very unsafe to speak decidedly as to the character of either the ribs or their articular facets.

So far as these specimens go, then, they favour the idea that *P. Hawkinsii* has 31 vertebræ cervical in Prof. Owen's sense of the term, and they assuredly do not countenance the notion that these vertebræ may vary in the same species. But if *Plesiosaurus Hawkinsii* has 54 or 56 cervico-dorsal vetebræ, and if 31 of these are cervical, then *P. Etheridgii* differs from it in the following particulars :—

1. The number of cervical vertebræ is at least one less.
2. The number of cervico-dorsal vertebræ is one or three less.
3. The head is shorter in proportion to the body.
4. The head is shorter in proportion to the neck.

I think then there can be no doubt as to the specific distinctness of *P. Etheridgii* from all the *Plesiosauri* as yet mentioned.

With regard to the other species, I judge from the descriptions and from such specimens as I have seen, that *P. Etheridgii* is very different from *megacephalus*, *macromus*, *pachyomus*, *arcuatus*, *sub-trigonus*, *trigonus*, *brachyspondylus*, *costatus*, *dœdicomus*, *rugosus*, *trochanterius*, and *affinis*. I doubt at present whether it would be possible to distinguish the detached vertebræ of *P. Etheridgii* from those of *P. Hawkinsii*; but I believe, having examined the series of vertebræ in the College of Surgeons' Museum, on which some fourteen species have been founded, they are all different from those of *P. Etheridgii.*

The measurements of the different parts are as follows, in inches and tenths :—

Head.

	in.	tenths.
From end of intermaxillary to end of occipital condyle	6	5
End of intermaxillary to anterior margin of orbit	2	15
End of intermaxillary to anterior end of parietal foramen	4	2
Width of orbit	1	2
Length (oblique longest diameter)	1	5
Extreme length of head from end of intermaxillary to end of quadratum	6	8

Neck.

Length of first seventeen cervical vertebræ, measured along their bodies	12	9
Length of following thirteen	15	1
Giving as entire length of neck	28	0

	in.	tenths
Sixteenth cervical vertebra.		
Centrum.—Longitudinal diameter	0	9
Vertical to base of neurapophysis[1]	1	1
Thence to top of neural spine	1	4
Neural spine vertically	0	8
Neural spine longitudinally	0	7
Costal pit.—Longitudinal measure	0	5
Vertical measure	0	3
Costal pit to base of neurapophysis	0	6
Dorsal region.—Total length	26	5
Sixth dorsal vertebra.		
Centrum.—Longitudinally	1	25
Vertically (anterior face)	1	3
Transversely	1	6
Neural spine.—Vertically	2	1
Longitudinally	0	9
Transverse process.—Length	0	75
Antero-posterior diameter	0	5
Vertical diameter	0	75
Sacral region.—Total length	2½ in.	
First sacral vertebra.		
Centrum.—Vertically	1	3
Transversely	1	65
Upper edge of centrum to summit of neural spine	2	2
Neural spine—Vertically	1	55
Longitudinally (about)	0	7
Lower edge of body to origin of transverse process	0	75
Thickness of transverse process	0	82
Length	0	25
Sacral rib.—Length	1	3
Thickness of distal end	0	6
Caudal region.—Total	26	0
Eleventh caudal vertebra.		
Centrum.—Length	0	9
Vertical	1	15
Transverse	1	35
From upper edge of centrum to summit of neural spine	2	8
Length of neural spine.—Vertically (about)	1	1
Longitudinally	0	65
Ribs.—11th measured along its curve	11	0
Diameter of head	0	7
Diameter of body	0	45
Humerus.—Long	7	2
Thickness of anterior end from above downwards	1	9
Expanded distal end—long	3	3
Expanded distal end—thick	0	5
Femur.—Long	7	15
Anterior extremity from above downwards	1	8

[1] Reckoned as the deepest part of the depression under the zygapophysis, no suture being visible.

The Structure of the Atlas and Axis.

Thanks to the investigations of Sir Philip Egerton, the structure of the axis and atlas of *Ichthyosaurus* is placed beyond doubt. But our knowledge of the corresponding parts of *Plesiosaurus* cannot be said to be by any means so well based, since it rests, so far as I am aware, upon the examination of a single and imperfect specimen, which has been described in the following terms by Professor Owen :—

"A recent opportunity of examining the atlas and axis of the *Plesiosaurus*, kindly afforded me by my friend Professor Sedgwick, has not only strengthened this view of the general nature of the 'subvertebral wedge-bones,' but has made me incline to the second hypothesis of the special homology of the first or anterior of the wedge-bones which is proposed in my 'Report on British Fossil Reptiles,' viz. :—That it answered to the part described as the body of the atlas, in the existing Saurians and Chelonians ; which therefore may be regarded, like the first subvertebral wedge-bone, as the cortical part only of such vertebral body, like the plate of bone beneath the biconcave central part of the body of the atlas in the Siluroid fish.

"The atlas and axis in the *Plesiosaurus* (fig. 3) preserve the general proportions of the other cervical vertebræ, and are consequently longer than their homologues in the *Ichthyosaurus* ; but they are similarly anchylosed together, and measure $4\frac{1}{2}$ centimetres (nearly 2 inches) in length, 3 centimetres across the anterior concave surface of the atlas, and $3\frac{1}{2}$ centimetres across the less concave posterior surface : the neural arch of each vertebra has coalesced with its centrum, and a long obtuse process is formed below by a similar coalescence of the first and second wedge-bones with each other and their respective centrums. The limits of the anterior wedge-bone, *c a*, *e x*, are traceable : it is proportionally larger than in the *Ichthyosaurus* (fig. 2), in which it is likewise larger than the succeeding wedge-bones. It forms in the *Plesiosaurus* the lower third part of the atlantal cup for the occipital condyle B *c a*, *e x* : the anchylosed bases of the neurapophyses (*n a*) form the upper border of the cup, and the intermediate part or bottom of the cavity is formed by the centrum of the atlas (*c a*), or rather by that part which, like the biconcave centrum in the Siluroid fish, is developed from the central portion of the notochord.

"The smaller or second wedge-bone (*c x*, *e x*) is lodged in the inferior interspace between the atlas and axis, but has coalesced with both bones, as well as with the large anterior wedge-bone or cortical part

of the body of the atlas, *c a*, *e x*. This anterior wedge-bone developes a thick but short, rough tuberosity from its under part, but there is no distinct second tuberosity from the second wedge-bone; both indeed have so coalesced together, as to parallel the continuous ossification of the under part of the notochordal capsule beneath the central parts of the bodies of the axis and atlas in the Siluroid fish (fig. 1, *c a e x*, *c x e x*, &c.). There is no transverse process from the centrum of the atlas of the *Plesiosaurus*; but the fractured base of a depressed parapophysis, *p* (lower transverse process), or anchylosed rib, projects from each side of the proper centrum of the axis."—(Professor Owen on the Atlas, Axis, and Subvertebral Wedge-bones in the *Plesiosaurus*.—Annals Nat. Hist. vol. xx. p. 219, 1847.)

This is all the evidence of the nature of the atlas and axis in *Plesiosaurus* which is given in the paper quoted, its author seeming not to be aware that important materials for checking his conclusions were offered by the specimens of *Plesiosaurus Hawkinsii* which he had already described. This is the more to be regretted, as the structure of these specimens is to my mind quite irreconcilable with Professor Owen's views.

What I have observed in *Plesiosaurus Etheridgii* and in *Plesiosaurus Hawkinsii* leads me, in fact, to form a very different conception of the structure of the atlas from that just cited.

Viewed in front, the deep hemispherical articular cup of the atlas of *Plesiosaurus Etheridgii* is seen to be divided by a triradiate mark (formed by the limestone of the matrix) into three portions; of these, one is inferior, the other two lateral and superior. The inferior piece I take to correspond with the so-called anterior or first wedge-bone of *P. pachyomus*; but it forms a more considerable portion of the articular cup than in the latter case, if I may judge by the figure. Viewed anteriorly, this inferior piece has a semicircular contour, while seen from below its anterior edge is straight, and the posterior produced laterally into a sort of cornu which overlaps the sides of a second so-called "subvertebral bone." The posterior margin is much excavated in the middle, receiving the convex anterior contour of this second "subvertebral bone."

The supero-lateral pieces are separated by an interval in the median line, wider than the close suture between them and the first wedge-bone. At the bottom of this interval a small portion of bone appears, which I believe to belong to the os odontoideum.

After contributing their share towards the articular cup for the occipital condyle, the supero-lateral pieces bend backwards so as to overlap the anterior zygapophyses of the axis. They seem to ter-

minate above by a smooth and rounded edge. The antero-lateral margin of these portions of the atlas is nearly straight, the upper third or thereabouts being inclined at a great angle to the rest: the postero-lateral margin is greatly excavated, on account of the backward projection of the supero-lateral pieces above and of the cornua of the inferior piece below. The body of the axis is concave posteriorly, the sides are convex from above downwards. Below it is rather concave from behind forwards. Its posterior margin is straight; the anterior is also straight, except for a short distance inferiorly, where it is much bevelled off. Traces of a rib, which probably articulated with the os odontoideum, exist on both sides of the anterior part of the body of the axis.

Between its anterior edge and the posterior excavated margin of the parts of the atlas just described, there is an interspace of $\frac{1}{5}$th of an inch. This is filled by a mass of bone with a convex edge, and separated by a deep groove from the axis and the rest of the atlas. Superiorly this bony mass is overlapped by the supero-lateral piece of the atlas—inferiorly by one of the cornua of the inferior piece; but on cutting this cornu away, I found it rested on a sort of articular face furnished by the inferior continuation of the bony mass. But this passed below, without any visible line of demarcation, into the second "subvertebral" bone. This bone is convex below and in front (where it fits into the excavated margin of the inferior piece of the atlas), and behind slopes backwards to articulate with the bevelled face of the axis.

I have nowhere seen the structure of the anterior articular cup, and the sutures which unite the supero-lateral and inferior pieces of the atlas, displayed as they are in this specimen;[1] but many of the other peculiarities are as well shown in one or other of the specimens of *P. Hawkinsii* in the British Museum.

Thus the under surfaces of the atlas and axis are exhibited in the specimen I have called No. 1. They are a good deal broken away, so as to display a longitudinal and nearly horizontal section of these vertebræ. The axis has nearly the same form and size as in *P. Etheridgii*; the inferior piece of the atlas appears to be bent upwards, and to be broken inferiorly and posteriorly; but between the two is seen a thin bony disk, not more than a third as long as the axis, and whch I take to be the section of the bony plate-like mass interposed between the axis and the three anterior pieces of the atlas in *P. Etheridgii.* No. 2 shows the right side of the axis and atlas very

[1] I may observe, that I performed all the more delicate operations required in bringing out these parts myself.

well, but the latter is somewhat crushed and distorted; nevertheless the anterior concavity is well seen. The suture between the cortical and neurapophysial portions is not traceable; the latter slopes back as in *P. Etheridgii*, and is visible on the left as well as on the right side. The peripheral piece appears to be prolonged anteriorly instead of posteriorly, but I believe this to arise from crushing merely.

The edge of an interposed bony plate is seen, as in *P. Etheridgii*, between the posterior edge of the three anterior portions of the atlas and the body of the axis. The neural spine of the axis is long and recurved; there is a rib with a short and broad head, which is articulated for the greater part of its extent either with the axis, or more probably with the os odontoideum; its anterior angle extends forwards as far as the inferior piece of the atlas.

Putting these different views and sections of the atlas and axis of *Plesiosaurus* together, it seems to me that they are consistent with only the following interpretation:—

1. The atlas and axis are, as Prof. Owen states, anchylosed.

2. What I have called the inferior piece of the anterior part of the atlas, corresponds with what Prof. Owen terms the anterior subvertebral wedge-bone; but I find its shape to be exceedingly different from that ascribed to the corresponding piece in *P. pachyomus*.

3. The sutures between this and the supero-lateral pieces are situated at a higher level on the face of the articular cup in *P. Etheridgii*. They are here, in fact, radii from the centre of that cup, while in the figure of *P. pachyomus* the sutures meet below the centre.

4. Prof. Owen describes no distinct supero-lateral pieces or median suture; and, not having seen them, he considers the upper two-thirds of the cup to be formed by a distinct mass, with which the neurapophyses have coalesced. In *P. Etheridgii* this mass is certainly nothing more than the bases of the neurapophyses themselves, which contribute, as in the Crocodile, to form the articular surface for the occipital condyle.

5. Prof. Owen conceives that the upper two-thirds of the articular cup (all but its extreme margin?) constitute the homologue of the os odontoideum, which is (as Rathke[1] proved eighteen years ago) simply the separately ossified central portion of the body of the atlas;

[1] Rathke, 'Entwickelungs-geschichte der Natter,' 1839, pp. 119, 120; also 'Ueber die Entwickelung der Schildkröten,' 1848. In the former essay Rathke says of the "processus odontoideus," "Therefore this process is not an outgrowth of the epistropheus, but the body of the atlas; while that bone which is reckoned as the first cervical vertebra is not a perfect vertebra, having no true body. What is called its body is nothing but a modified inferior spinous process."

the so-called body of that bone (the homologue of the inferior piece in the *Plesiosaurus*) being a distinct peripheral ossification.

I have just shown, however, that in *P. Etheridgii* the os odontoideum must be sought elsewhere, and I have not the slightest doubt that it is that osseous plate whose convex lateral edges are seen between the anterior portions of the atlas and the axis, and which ends below in the so-called second subvertebral bone.

6. I have not as yet met with any neural spine in the atlas of *Plesiosaurus* corresponding with the flattened and separate homologue of this part of a vertebra which is found in the atlas of the Crocodile; but the complete correspondence of the *Plesiosaurian* atlas and axis (in this reading of their structure) with those of the *Crocodilia* is highly interesting, as it harmonizes perfectly with the strongly crocodilian affinities manifested by many other parts of the organization of the *Plesiosaurus*. I reserve a lengthened comparison of the two structures for my Memoir, merely adding that Cuvier found the atlas and axis of his "Crocodile d'Honfleur" (a Teleosaurian) "soudés ensemble," the posterior face of the axis being concave;[1] and that, according to Von Meyer's figures, the atlas and axis of *Nothosaurus* were very similar to those of *Plesiosaurus*.[2]

The Structure of the Cranium.—The length to which these remarks have already extended, and the impossibility of rendering any account of the structure of the cranium intelligible without a large number of illustrations (which will be more fitly reserved for my forthcoming memoir), lead me to throw what I have to say into a few propositions, whose full proof will be adduced hereafter.

1. The structure of the Plesiosaurian cranium is best to be understood by comparing it with that of *Teleosaurus*,[3] when its numerous crocodilian affinities become at once apparent.

[1] 'Ossemens Fossiles,' ed. 4, t. ix. pp. 306–7.

[2] Hermann von Meyer says ('Die Saurier des Muschelkalkes') of *Nothosaurus*: "The atlas had a remarkably depressed superior arch, whose spinous process was inclined backwards at an angle of about 25°. The posterior articular processes were directed backwards; and below, a short lateral part, analogous to a hook-like cervical rib, appears to have been attached. . . . . The atlas and axis do not seem to have been anchylosed" (p. 30). On comparing Von Meyer's figures, the similarity of the atlas and axis to those of *Plesiosaurus* is remarkable. The interspace left between the axis and atlas corresponds to that for the os odontoideum, and the projecting piece figured at the lower anterior edge of the axis may, I think, very possibly be the free lower end of the os odontoideum.

[3] My statements respecting the structure of the skull of *Teleosaurus* are based on my examination of two very beautiful specimens of *T. temporalis* in the Tesson Collection, now in the British Museum. I am informed that these crania were worked out from the matrix by M. Selys Deslongchamps, to whom therefore the credit of the discovery of any new points s properly due.

2. In the *Teleosauria* (*Teleosaurus temporalis*) there is a singular aperture closely resembling in form and position the external nostril of the *Plesiosaurus*, though in the *Teleosauria* there is every reason to believe that the nostrils were, as in the Gavials, at the end of the snout. The bony margins of the aperture are, however, somewhat differently constituted in the two genera.

3. In the *Teleosaurus* the jugal bone is long and slender. In *Plesiosaurus Etheridgii* and others, I find a bony style of greater or less length, broken posteriorly, but having otherwise precisely the same relations and form as the jugal of the *Teleosaurus*.[1] This process is particularly well shown in a cranium (named *P. dolichodeirus*) in the Museum of the Society, and is figured by Mr. Conybeare in his restoration.

4. Contrary to what is commonly stated, the post-frontal appears to me, in *P. Etheridgii* and *Hawkinsii* at any rate, to articulate with a bone, the homologue of the squamosal [2] of the Crocodile.

5. The squamosal of the *Plesiosaurus* seems to have been confounded by some with a process of the parietal.

6. The temporal fossa is divided by the post-frontal in the manner so characteristic of, though not absolutely peculiar to, the Crocodilian reptiles. The great superior fossæ correspond with the large superior temporal fossæ of the Teleosaurian, and even the narrowness and crested form of the upper surface of the parietal (supposed to be distinctive of the *Plesiosaurus*) are very closely approached in such *Teleosauria* as *T. temporalis*.

7. The exoccipital sends outwards and downwards a process which reaches the great quadratum, and between this below, the quadratum externally, and the squamosal above, there is a large aperture in the *Plesiosaurus*.

In the triassic *Enaliosauria*, however, the corresponding interval is, judging by Hermann von Meyer's figures of *Nothosaurus*, smaller in proportion, or, as in *Simosaurus*, absent (?). On the other hand, it is larger in the *Teleosauria* than in the existing *Crocodilia*.

8. The basi-sphenoid appears upon the base of the skull for a great space in the *Plesiosaurus*, while in the ordinary Crocodile it is not visible at all, being hidden by the pterygoids. Even in the Gavial, however, the basi-sphenoid shows itself fully on the base of the skull, while in the *Teleosaurus* it is as much exposed as in the

[1] Hermann von Meyer figures a very similar process in *Simosaurus*, pl. 65, figs. 1 & 2.

[2] This is the bone commonly but erroneously termed the "mastoid" in the Crocodile. Rathke and Hallman have long since satisfactorily shown that the homologous bone has no relation with the true mastoid.

Plesiosaurus, and presents a median ridge with a deep fossa on either side. There are a similar ridge and fossæ in *Plesiosaurus*, the latter having, I imagine, been mistaken for the posterior nares.

9. I believe the posterior nares were situated far forwards in the *Plesiosaurus*; for in the first place, the object of their being situated as in the Crocodile is not intelligible teleologically: and on morphological grounds we should expect to find them anteriorly situated, for the Gavial has them more forward than the Crocodile, and the *Teleosaurus* than the Gavial. In the latter, indeed, they are so far forward, that the pterygoids do not enclose them below at all. They are nearly on a line with the middle of the orbits.

10. The pterygoids of the *Plesiosaurus* send processes backwards to abut against the quadratum.[1] The ends of the corresponding bones are broken off in the *Teleosauria* I have examined.

11. The descending process of the basi-occipital is single in the ordinary Crocodile, but in the *Teleosaurus* it is divided into two widely separated tubercles as in *Plesiosaurus*.

12. The supra-occipital is widely separated from the edge of the occipital foramen by the exoccipitals in the Crocodile. In the *Teleosaurus* it comes close to that edge. In the *Plesiosaurus* it forms part of it.

13. The petrosal bone is covered externally by the quadratum in the Crocodile. In the *Teleosaurus* it is almost completely exposed as in the *Plesiosaurus*.

These facts seem to me to have an especial interest when we consider the palæontological relations of the *Teleosauria* to the long-necked *Enaliosauria*, on the one hand, and to the *Crocodilia* on the other. Anatomically, as chronologically, the Teleosaurian bridges over the gap between *Nothosaurus* and *Alligator*.

[1] These processes are particularly well shown in the very instructive specimen labelled 14,550 in the British Museum. I propose to figure this as well as some others in my Memoir.

L

ON THE THEORY OF THE VERTEBRATE SKULL

Being the Croonian Lecture delivered before the Royal Society, June 17, 1858

Roy. Soc. Proc., vol. ix., 1857–59, *pp.* 381–457; *Ann. Nat. Hist., vol. iii.*, 1859, *pp.* 414–439

THE necessity of discussing so great a subject as the Theory of the Vertebrate Skull in the small space of time allotted by custom to a lecture, has its advantages as well as its drawbacks. As, on the present occasion, I shall suffer greatly from the disadvantages of the limitation, I will, with your permission, avail myself to the uttermost of its benefits. It will be necessary for me to assume much that I would rather demonstrate, to suppose known much that I would rather set forth and explain at length; but on the other hand, I may consider myself excused from entering largely either into the history of the subject, or into lengthy and controversial criticisms upon the views which are, or have been, held by others.

The biological science of the last half-century is honourably distinguished from that of preceding epochs, by the constantly increasing prominence of the idea, that a community of plan is discernible amidst the manifold diversities of organic structure. That there is nothing really aberrant in nature; that the most widely different organisms are connected by a hidden bond; that an apparently new and isolated structure will prove, when its characters are thoroughly sifted, to be only a modification of something which existed before,—are propositions which are gradually assuming the position of articles of faith in the mind of the investigators of animated nature, and are directly, or by implication, admitted among the axioms of natural history.

And this is not wonderful; for no living being can be attentively

studied without bearing witness to the truth of these propositions. The tyro in comparative anatomy cannot fail to be struck with the resemblances between the leg and the jaw of a crustacean ; between the parts of the mouth of a beetle and those of a bee ; between the wing of the bird and the fore-limb of the mammal. Everywhere he finds unity of plan, diversity of execution.

Or again, how can the intelligent student of the human frame consider the backbone, with its numerous joints or vertebræ, and trace the gradual modification which these undergo downwards into the sacrum and coccyx, and upwards into the atlas and axis, without the notion of a vertebra in the abstract, as it were, gradually dawning upon his mind ; the conception of an ideal something which shall be a sort of mean between these various actual forms, each of which may then easily be conceived as a modification of the abstract or typical vertebra ?

Such an idea, once clearly apprehended, will hardly permit the mind which it informs to rest at this point. A glance at a section of that complex bony box formed by the human skull and face, shows that it consists of a strong central mass, whence spring an upper arch and a lower arch. The upper arch is formed by the walls of the cavity containing the brain, and stands in the same relation to it, as does the neural arch of a vertebra to the spinal cord, with which that brain is continuous. The lower arch encloses the other viscera of the head, in the same way as the ribs embrace those of the thorax. And not only is the general analogy between the two manifest but a young skull may be readily separated into a number of segments, in each of which it requires but little imagination to trace a sort of family likeness to such an expanded vertebra as the atlas.

What can be more natural then than to take another step—to conceive the skull as a portion of the vertebral column still more altered than the sacrum or the coccyx, whose vertebræ are modified in correspondence with the expansion of the anterior end of the nervous centre and the needs of the cephalic end of the body, just as those of the sacrum are fashioned in accordance with the contraction of the nervous centre and the mechanical necessities of the opposite extremity of the frame ?

Two generations have passed away since, perhaps, by some such train of reasoning as this, such a conception of the nature of the vertebrate skull arose in the mind of the philosophic poet, Goethe ; and a somewhat shorter period has elapsed since a poetical, or perhaps I might more justly say a fanciful, philosopher, Oken, published a "Theory of the Skull" embodying such a conception ; and since

the excellent Dumeril allowed a like hypothesis to be strangled in the birth by the small wit of a French academician.

The progress of modern science is so rapid, that one is unaccustomed to see half a century elapse after the promulgation of a doctrine, which is capable of being tested by readily accessible facts, without either its firm establishment or its decisive overthrow. But nevertheless, at the present day, the very questions regarding the composition of the skull, which were mooted and discussed so long ago by the ablest anatomists of the time, are still unsettled ; the theory of the vertebrate skull is one of the most difficult and, apparently inextricably confused subjects, which the philosophic anatomist can attack, and in consequence, not a few workers in science look, somewhat contemptuously, upon what they are pleased to term mere hypothetical views and speculations.

Indeed, though the germ of a great truth did really lie in these same hypotheses, its late or early development into a sound, and consequently fruitful, body of doctrine depended upon the manner in which biologists set about solving the problem presented to them ; upon the clearness with which they apprehended the nature of the questions they wished to put, and the consequent greater or less fitness of the method by which their interrogation of nature was conducted.

I apprehend that it has been and is, too often forgotten that the phrase " Theory of the Skull " is ordinarily employed to denote the answers to two very different questions ; the first, Are all vertebrate skulls constructed upon one and the same plan ?—the second, Is such plan, supposing it to exist, identical with that of the vertebral column ?

It is also forgotten that, to a certain extent, these are independent questions ; for though an affirmative answer to the latter implies the like reply to the former, the converse proposition by no means holds good ; an affirmative response to the first question being perfectly consistent with a negative to the second.[1]

As there are two problems, so there are two methods of obtaining their solution. Employing the one, the observer compares together

[1] There is a wide difference, too, in the relative importance of either question to the student of comparative anatomy. Unless it can be shown that a general identity of construction pervades the multiform varieties of vertebrate skulls, a concise, uniform, and consistent nomenclature becomes an impossibility, and the anatomist loses at one blow the most important of aids to memory, and the most influential of stimulants to research. The second question, on the other hand, though highly interesting, might be settled either one way or the other without exerting any very important influence on the practice of comparative anatomy.

a long series of the skulls and vertebral columns of adult *Vertebrata*, determining, in this way, the corresponding parts of those which are most widely dissimilar, by the interpolation of transitional gradations of structure. Using the other method, the investigator traces back skull and vertebral column to their earliest embryonic states, and determines the identity of parts by their developmental relations.

It were unwise to exalt either of these methods at the expense of its fellow, or to be other than thankful that more roads than one leads us to the attainment of truth. Each, it must be borne in mind, has its especial value and its particular applicability, though at the same time it should not be forgotten, that to one, and to one only, can the *ultimate* appeal be made, in the discussion of morphological questions. For seeing that living organisms not only *are*, but *become*, and that all their parts pass through a series of states before they reach their adult condition, it necessarily follows that it is impossible to say, that two parts are homologous or have the same morphological relations to the rest of the organism, unless we know, not only that there is no essential difference in these relations in the adult condition, but that there is no essential difference in the course by which they arrive at that condition. The study of the gradations of structure presented by a series of living beings may have the utmost value in suggesting homologies, but the study of development alone can finally demonstrate them.

Before the year 1837, the philosophers who were occupied with the Theory of the Skull confined themselves, almost wholly, to the first-mentioned mode of investigation, which may be termed the "method of gradations." If they made use of the second method at all, they went no further than the tracing of the process of ossification, which is but a small, and by no means the most important part of the whole series of developmental phenomena, presented by either the skull or the vertebral column.

But between the years 1836 and 1839, the appearance of three or four remarkable Essays, by Reichert, Hallmann, and Rathke,[1] inaugurated a new epoch in the history of the Theory of the Skull. Hallmann's work on the Temporal Bone is especially remarkable for the mass of facts which it contains, and for that clearness of insight

[1] The titles of these works are,—Reichert, 'De Embryonum arcubus sic dictis Branchialibus,' 1836, which I have not seen; the same writer's essay, 'Ueber die Visceralbogen der Wirbelthiere im Allgemeinen,' Müller's Archiv, 1837. Hallmann, 'Die vergleichende Osteologie des Schläfenbeins,' 1837. Rathke, 'Entwickelungsgeschichte der Natter,' 1839. I regret that, in spite of all efforts, I have hitherto been unable to procure a copy of another very important work of Rathke's, the 'Programm,' contained in the 'Vierter Bericht von dem naturwissenschaftlichen Seminär zu Königsberg.'

into the architecture of the skull, which enabled him to determine the homologies of some of the most important bones of its upper arch throughout the vertebral series. Rathke showed the singular nature of the primordial cranial axis, and Reichert pointed out in what way alone the character of its lower arches could be determined. For the first time, the student of the morphology of the skull was provided with a criterion of the truth or falsity of his speculations, and that criterion was shown to be Development.

My present object is to lay before you a brief statement of some of the most important results to which the following out of the lines of inquiry opened up by these eminent men seems to lead. Much of what I have to say is directed towards no other end than the revival and justification of their views—a purpose the more worthy and the more useful, since with one or two honourable exceptions—I allude more particularly to the recent admirable essays of Prof. Goodsir—later writers on the Theory of the Skull have given a retrograde impulse to inquiry, and have thrown obscurity and confusion upon that which twenty years ago had been made plain and clear.

I have said that the first question which offers itself is, whether all vertebrate skulls are or are not, constructed upon a common plan, and in entering upon this inquiry I shall assume (what will be readily granted), that if it can be proved that the same chief parts, arranged in the same way, are to be detected in the skulls of a Sheep, a Bird, a Turtle, and a Carp, the problem will be solved affirmatively, so far, at any rate, as the osseous cranium is concerned.

Composition of the Skull of a Sheep (fig. 1).

On examining a section of the cranium of a sheep, made either along a vertical and longitudinal, or a transverse and horizontal plane, a more or less completely ossified mass is observed in the middle line below, which forms part of the floor of the cranial cavity, but extends beyond it. This may be termed the 'craniofacial axis.' Posteriorly it is a broad plate flattened from above downwards, and is nearly parallel with the long axis of the cranial cavity; but from a point immediately behind the sella turcica, it becomes thicker and is compressed from side to side, so that, at the anterior boundary of the sella turcica, the craniofacial axis is much deeper than wide, and assumes the form of a vertical plate. From the anterior boundary of the cranial cavity onwards, or in its facial portion, the axial plate is very deep and very thin, and a line drawn through its longitudinal

axis would cut that of the cranial cavity at a very considerable angle. The craniofacial axis then is naturally divisible into three regions; a middle thick part, lodging the sella turcica, and composed of the basisphenoid behind and presphenoid in front, the two being separated by a suture; a posterior, lamellar, horizontally-flattened part, forming in the young animal a distinct bone, the basioccipital, bounding the occipital foramen behind and uniting with the basisphenoid in front; and an anterior laterally compressed portion, composed of the bony "lamina perpendicularis" of the ethmoid above and behind, united by the cartilaginous septum narium to the bony vomer below.

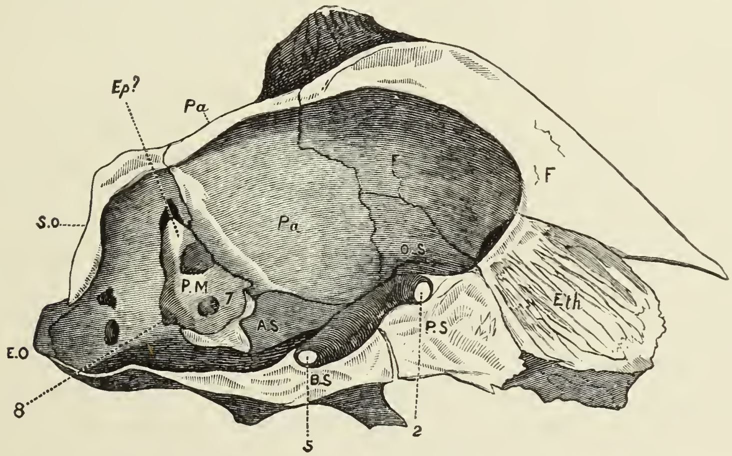


Fig. 1.—Longitudinal section of the Skull of a Sheep. In this and the following sections of Crania the letters have the same meaning.

B.O. Basioccipital.
B.S. Basisphenoid.
P.S. Presphenoid.
Eth. Ethmoid (lamina perpendicularis).
E.O. Exoccipital.
M. Mastoid.
P. or P.S. Petrosal.
P.M. Petromastoid.

A.S. Alisphenoid.
O.S. Orbitosphenoid.
Pf. Prefrontal.
Sq. Squamosal.
Ep. Epiotic.
S.O. Supraoccipital.
Pa. Parietal.
F. Frontal.

Foramina for nerves.
1. Olfactory; 2. optic; 3 & 4. oculomotor and pathetic nerves; 5. third division of trigeminal; 7. portio dura and mollis; 8. pneumogastric; Epiph. Pineal gland, or epiphysis cerebri.

This anterior division of the axis may be termed its ethmovomerine portion. Its posterior edge helps to close the anterior outlet of the cranial cavity, from which it is otherwise completely excluded.

The sella turcica lodges the pituitary body, and the synchondrosial union between the basisphenoid and presphenoid is situated so far forwards that the anterior wall of the fossa is almost wholly formed by the rostrum-like anterior prolongation of the basisphenoid. The

spinal cord passes out behind the posterior margin of the basioccipital. The olfactory nerves leave the skull on each side of the ethmovomerine division of the craniofacial axis.

The walls of the cranial cavity are formed by a number of bones, which are divisible into two series, a superior and a lateral. Of the latter, four pairs of bones, separated by natural lines of demarcation, or sutures, are distinguishable, three of which abut directly upon the cranio-facial axis, while the fourth pair are only indirectly connected with it. Behind are the exoccipitals,[1] united with the basioccipital, and forming the lateral boundaries of the occipital foramen. In front of these are the petromastoids, complex bones which contain the auditory labyrinth, and are connected with the anterior part of the basioccipital and the posterior and superior part of the basisphenoid, only by cartilage.

Next come the alisphenoids, which are attached to the infero-posterior and the anterior portions of the basisphenoid. And, lastly, the orbitosphenoids articulate with the upper margins of the vertically elongated presphenoid.

In the superior series only four bones can be counted, of which two are single and two are pairs. The hindermost is the supra-occipital bone. It articulates with both the exoccipitals and the petromastoids. The next, in front, is the parietal, single in the adult sheep, but composed of two symmetrical halves in the lamb. It articulates with the petromastoids and with the alisphenoids. The frontals, or anterior paired bones, lastly, unite with the orbito-sphenoids, and, in front of them, with the ethmoid.

Most important relations exist between the contents of the cranium and these constituent elements of its walls. The par vagum makes its exit between the exoccipital and the petromastoid; the portio dura and portio mollis enter the petromastoid; the third division of the trigeminal passes through the large "foramen ovale," which, in the sheep, has the exceptional peculiarity of being situated nearly in the middle of the alisphenoid; the optic nerve passes through a foramen included between the orbito- and pre-sphenoids, while, as has been mentioned above, the olfactory nerve passes out beside the ethmoid and in front of the orbitosphenoid. The relation

[1] In speaking of these bones I shall avail myself, for the most part, of the useful translation of the Cuvierian nomenclature adopted by Prof. Owen. It is, doubtless, more convenient to say "alisphenoid" than "grande aile" or "aile sphenoidale," and "orbitosphenoid" instead of "aile orbitaire," the slightness of the real change thereby effected being one of its principal recommendations. The adoption of the terms will, of course, not be held to imply any recognition of the justice of the views of either their inventor or their adopter.

of the pituitary body, or hypophysis cerebri, to the upper surface of the basisphenoid, has already been alluded to; it, of course, gives more or less nearly the position of the third ventricle and crura cerebri. A style passed horizontally through the corpora quadrigemina, or mesencephalon, would strike against, or close to, the anterior margin of the petromastoid bone.

On turning to the exterior of the skull, certain bones come into view which were before invisible, as they take no share in forming the lateral walls of the cranial cavity, but are, as it were, stuck on to the outer surface of these walls. The principal of these is the great squamosal bone, applied to the outer surfaces of the petromastoid, parietal and alisphenoid bones, sending off its zygomatic process to unite with the jugal, and furnishing the articular surface for the condyle of the lower jaw.

Partly articulated with the squamosal and partly with the petromastoid, is the irregular capsule of the tympanic bone, to which the tympanic membrane is attached, on whose removal the ossicula auditûs come into view, consisting of the malleus, incus, and stapes. The processus gracilis of the first of these bones lies between the tympanic and the squamosal. The short process of the incus abuts against the inner wall of the tympanum, just below the squamosal and close to the line of junction of the petrous and mastoid. These are the leading points in the structure of the sheep's cranium to which I wish to direct attention at present. Bearing them in mind, let us now proceed to the consideration of the skull of a bird.

Composition of the Skull of a Bird (fig. 2).

In most adult birds, as is well known, the bones of the cranium have coalesced so completely as to be undistinguishable. But in the chick, and to a greater or less extent, in the adult struthious bird, the boundaries of the various bones are obvious enough; and I will therefore select for comparison with the mammalian skull that of an ostrich, and that of a young chicken.

The craniofacial axis of the bird has the same general figure as that of the sheep, consisting of a thick, solid, median portion, lodging the sella turcica; of a posterior, horizontally, and of an anterior, vertically, expanded division; but it is comparatively shorter and thicker in correspondence with the greater shortness, in proportion to its depth, of the cranial cavity. The sella turcica is very deep, and its front wall is very thick. The lower and anterior half of this wall is produced into a long tapering process, which extends forwards

far beyond the anterior limit of the bony lamina perpendicularis of the ethmoid, to end in a point.

Overlying this process, and articulated with more than the posterior half of its upper surface, there is, in the ostrich, a strong, thick, vertical, bony plate, narrower in front and behind than in the middle, and below than above. A curved vertical ridge on each lateral surface marks the line of its greatest transverse diameter, and seems to indicate a primitive division of the mass into two parts, an anterior and a posterior. The latter is connected above with the bony plates representing the orbitosphenoids. The former exhibits on each side, posteriorly and superiorly, a groove, in which the olfactory nerve rests and, above this, expands into an arched process, which supports the anterior extremity of the frontal bone.

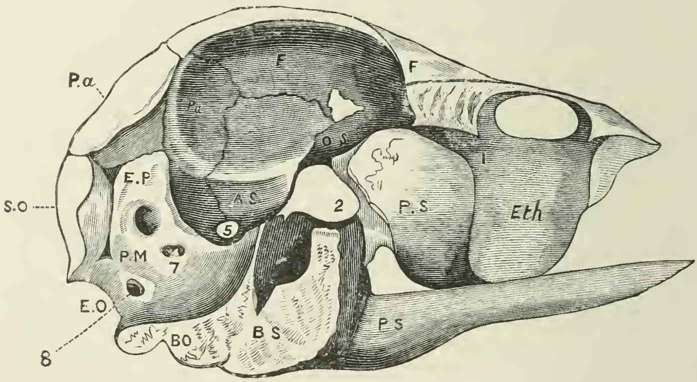


Fig. 2.—Longitudinal section of the Skull o. a young Ostrich.

Anteriorly, the superior end of the bone widens into a rhomboidal plate, which appears externally between the nasal bones. These anterior and posterior processes of the superior edge of the bone are connected by a delicate ridge, which passes from one to the other above, but leaves an irregular oval gap below.

The anterior edge of the bony plate in question is continued into the unossified septum narium, which below supports the delicate bony representative of the vomer.

In the chick, the whole of the parts just described are unossified, but the composition and structure of the rest of the axis is essentially the same as in the ostrich.

It is not difficult to identify in the craniofacial axis of the bird, parts corresponding with those which have been shown to exist in the mammal. In the chick, the basioccipital can be readily separated

from the basisphenoid. The latter has the same relation to the sella turcica in the bird as in the mammal; and only differs from it in that singular beak-like process, into which its inferior portion is prolonged anteriorly, and which is produced, according to Kölliker,[1] by the coalescence with the basisphenoid of a distinct ossification, which is developed in the presphenoidal cartilage and partially represents the presphenoid of the mammal. The rest of the presphenoidal cartilage is more or less completely ossified, and appears to be represented in the ostrich by that part of the "vertical bony plate" which lies behind the curved ridge referred to above; while that part of the plate which is situated in front of the ridge, answers to the lamina perpendicularis of the ethmoid.

Nothing can be more variable, in fact, than the mode in which the ossification of the presphenoidal and ethmoidal portions of the craniofacial axis takes place in birds; while nothing is more constant than the general form preserved by these regions, and their relation to other parts, irrespectively of the manner in which ossification takes place in them. And in these respects birds do but typify the rest of the oviparous *Vertebrata*.

If we compare the inferolateral walls of the ostrich's cranium with those of the sheep, we find the most singular correspondences. Posteriorly are the exoccipitals, which contribute to form the single condyloid head for articulation with the atlas, but otherwise present no important differences. In front of the exoccipital lies a considerable bony mass, which unites, internally and inferiorly, with the basioccipital and basisphenoid bones, and posteriorly is confluent with the exoccipitals. Its anterior margin is distinguishable into two portions, a superior and an inferior, which meet at an obtuse angle. The anterior inferior portion articulates with the alisphenoid; the anterior superior portion with the parietal. The anterior, posterior and inferior, relations of this bone are therefore the same as those of the petromastoid of the sheep.

Superiorly and posteriorly, a well-marked groove (which, however, is not a suture) appears to indicate the line of demarcation between the supraoccipital and this bone, whose pointed upper extremity appears consequently to be wedged in between the supraoccipital and the parietal.

The par vagum passes out between the bony mass under description and the exoccipital; the third division of the trigeminal leaves the skull between it and the alisphenoid. The portio dura and the portio mollis enter it by foramina very similarly disposed to those in

[1] 'Berichte von der Königlichen Zool. Anstalt zu Würzburg,' 1849, p. 40.

the sheep. Superiorly there is a fossa on the inner face of the bone, which corresponds with a more shallow depression in the sheep, and, like it, supports a lobe of the cerebellum. Finally, the anterior inferior edge of the bone traverses the middle of the fossa which receives the mesencephalon. In every relation of importance, therefore, this bony mass corresponds exactly with the petromastoid of the sheep, while it differs from it only in its union with the exoccipitals and the supraoccipital posteriorly, and its contact with the craniofacial axis below.

If from the ostrich we turn to the young chick (fig. 3), the condition of this part of the walls of the skull will be found to be still more instructive. The general connexions of the corresponding bony mass, Pt. M. Ep., are as in the ostrich; but while it is even more evident that the groove appearing to separate its upper end from the supraoccipital is no longer a real suture (whatever it may have been), a most distinct and clear suture, of which no trace is visible in the ostrich's skull, traverses the bone at a much lower point, dividing it into an inferior larger piece, united with the exoccipital, and a superior portion, anchylosed with the supraoccipital. The latter contains the upper portions of the superior and external semicircular canals.

Moreover, on endeavouring to separate the inferior bone from the exoccipital, it readily parts along a plane which traverses the fenestra ovalis externally, and the anterior boundary of the foramen of exit of the par vagum internally. The posterior smaller portion remains firmly adherent to the exoccipital, while the other larger portion comes away as a distinct bone.

The latter answers exactly to the mammalian petrosal, while the small posterior segment corresponds with the mammalian mastoid. Like that of the mammal, it is eventually anchylosed with the petrosal; but unlike that of the mammal, it is also, and indeed at an earlier period, confluent with the exoccipital.[1]

Thus, to return to the ostrich's skull, the bony mass interposed between the exoccipital, supraoccipital and parietal bones, and the craniofacial axis, is in reality composed of three bones, an anterior, petrosal, a posterior, mastoid, and a third, which is distinct from the petrosal and mastoid in the chick, but is anchylosed with them in the ostrich, and which has as yet received no name. I shall term it, from its position with respect to the organ of hearing, the epiotic bone, "os epioticum."[2]

[1] See Note I.

[2] My reasons for considering this osseous element to be distinct from the supraoccipital will be given below.

The homology of the bone here called petrosal, with that of the mammal, is admitted by all anatomists. The bone which lies immediately in front of the petrosal is, with a no less fortunate unanimity, admitted to be the homologue of the mammalian alisphenoid. But it is worthy of particular remark, in reference to the shifting of the relative positions of the lateral elements of the cranial wall, which has been imagined to take place in the ovipara, in consequence of the supposed invariable disappearance of the squamosal from the interior of their skulls ; that although precisely the same bones are visible on the inner surface of the cranial cavity in the ostrich as in the sheep, the squamosal being absent in both, yet in the ostrich the third division of the trigeminal does not pass through the middle of the alisphenoid, but between it and the petrosal.[1]

The orbitosphenoids appear like mere processes of the presphenoid, and their relation to the optic nerves is altered in the same way (when compared with the corresponding bones in the sheep) as that of the alisphenoids to the trigeminal, that is to say the nerves pass behind, and not through them.

The superior series of bones in the cranial wall is exactly the same as in the sheep, and the parietals are distinct in the young ostrich, as in the lamb.

Attached to the exterior of the skull of the ostrich are, as in the sheep, several bones ; but the appearance of some of these is widely different from that of the parts which correspond with them in the mammal. This is at least the case with the largest and uppermost of these bones, which lies upon the parietal above, the alisphenoid in front, and the exoccipital behind ; while internally it is in relation with the petromastoid.

This bone lies immediately above an articular surface, which is furnished to the os quadratum by the petrosal, and more remotely it helps to roof in the tympanic cavity but takes no share in the formation of the fenestra ovalis. It sends a free pointed process downwards and forwards, which does not articulate with the jugal. Except in this particular, however, the bone in question resembles in every essential relation the squamosal of the sheep, while to the same extent it differs from the mastoid of that animal.

I have stated that in the ostrich this bone does not appear upon the inner surface of the wall of the skull, and in this respect, while it resembles the squamosal of the sheep and Ruminants generally, it differs from that of most other *Mammalia*, in which the squamosal makes its appearance in the interior of the skull, between the parietal,

[1] See Note II.

frontal, alisphenoid and petrosal bones, and so contributes more or less largely to the completion of the cranial wall.

But it has been most strangely forgotten that the relations of the bone in question in birds, are by no means always those which obtain in the ostrich. In the young of the commonest and most accessible of domestic birds, in the chicken, the squamosal may be readily seen to enter largely into the cranial wall; a rhomboidal portion of its anterior and internal surface being interposed in front of the petrosal, between this bone, the parietal, the frontal, and the alisphenoid (Sq. fig. 3).

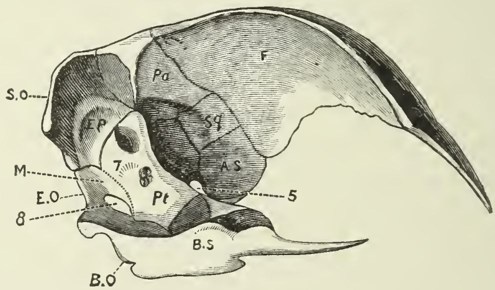


Fig. 3.—Longitudinal section of the Skull of a young Chicken.

There is therefore not a single relation (save the connexion of the jugal) in which this bone does not resemble the squamosal of the *Mammalia*—there is not one in which it does not differ from their mastoid.

The second bone applied externally to the cranium in the bird, is that large and important structure, the os quadratum, which intervenes between the petrosal and squamosal bones above, and the articular portion of the lower jaw below; which articulates with the pterygoid internally, and with the quadratojugal externally, which gives attachment to a part of the tympanic membrane, posteriorly, and which is very generally termed the tympanic bone, from its supposed homology with the bone so named in the *Mammalia*. The resemblance to the tympanic bone, however, hardly extends beyond its relation to the tympanic membrane; for in no other of the particulars mentioned above do the connexions of the two bones correspond. The tympanic of the mammal does *not* articulate with the lower jaw, nor with the pterygoid,[1] nor with the jugal or quadratojugal. On the other hand, if the connexions of the tympanic membrane were sufficient to determine the point, not only the quad-

[1] Though the pterygoid comes close to it in *Monotremata*.

ratum, but the articular element of the lower jaw, and even some cranial bones, must be regarded as tympanic.[1]

Again, if we trace the modifications which the tympanic bone undergoes in the mammalian series, we find that in those mammals, such as *Echidna* and *Ornithorhynchus*, which approach nearest to the *Ovipara*, and which should therefore furnish us with some hint of the modifications to which the tympanic bone is destined in that group, the bone, so far from increasing in size and importance, and taking on some of the connexions which it exhibits in the oviparous *Vertebrata*, absolutely diminishes and becomes rudimentary, so that the vast bony capsule of the placental mammal is reduced, in the monotreme, to a mere bony ring.

But it is no less worthy of remark, that in these very same animals the malleus and incus have attained dimensions out of all proportion to those which they exhibit in other mammals, and that they even contribute to the support of the tympanic membrane.

So far, therefore, from being prepared by the study of those *Mammalia* which most nearly approach the *Ovipara*, to find, in the most highly organised of the latter, an immense os tympanicum, with a vanishing malleus and incus, we are, on the contrary, led to anticipate the disappearance of the tympanicum, and the further enlargement of the ossicula auditûs. Thus far the cautious application of the method of gradations leads us, and leads us rightly—though the demonstration of the justice of its adumbrations can only be obtained by the application of the criterion of development.

It is twenty-one years since this criterion was applied by Reichert Since his results were published, they have been, in their main features, verified and adopted by Rathke, the first embryologist of his age; and yet they are ignored, and the quadratum of the bird is assumed to be the tympanic of the mammal, in some of the most recent, if not the newest discussions of the subject. Reichert and Rathke have proved, that in the course of the development of either a mammal or a bird, a slender cartilaginous rod makes its appearance in the first visceral arch, and eventually unites with its fellow, at a point corresponding with the future symphysis of the lower jaw. Superiorly, this rod is connected with the outer surface of the cartilage, in which the petrosal bone subsequently makes its appearance. Near its proximal end, the rod-like "mandibular cartilage" sends off another slender cartilaginous process, which extends forwards parallel with the base of the skull. With the progress of development, ossification takes place in the last-named cartilage, and

[1] See Note III.

converts it, anteriorly, into the palatine, and posteriorly, into the pterygoid bone. The mandibular cartilage itself becomes divided into two portions, a short, proximal, and a long, distal, by an articulation which makes its appearance just below the junction of the pterygo-palatine cartilage. The long distal division is termed, from the name of its original discoverer, Meckel's cartilage. It lengthens, and an ossific deposit takes place around, but, at first, not in it. The proximal division in the mammal ossifies, but usually loses its connexion with the pterygoid, remains very small and becomes the

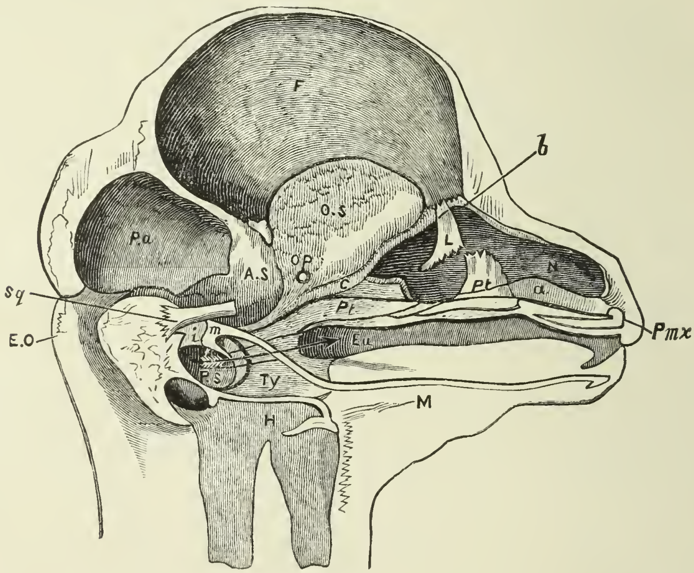


Fig. 4.—Dissection of the cranium and face of a Fœtal Lamb 2 in. long. The letters have the same signification as elsewhere, except N. Nasal capsules. *a. b. c.* Septum narium. L. Lacrymal. Pl. Palatine. Eu. Arrow indicating the course of the Eustachian tube. *i.* Incus. *m.* Malleus. M. Meckel's cartilage. H. Hyoid. Ps. Petrosal. Ty. Tympanic.

incus. In the bird the corresponding part enlarges, ossifies, and becomes the os quadratum, retaining its primitive connexion with the pterygoid. In the mammal, the proximal end of Meckel's cartilage ossifies and becomes the malleus, while the rest ultimately disappears. The ossific mass which is formed around Meckel's cartilage remains quite distinct from the proximal end of that cartilage, or the malleus. gradually acquires the form of the ramus of the lower jaw, and eventually developes a condyle which comes into contact and articulates with, the squamosal. In the bird, on the contrary, the ramus

of the jaw unites with the ossified proximal end of Meckel's cartilage ; which becomes anchylosed with the ramus, but retaining its moveable connexion with the quadratum (or representative of the incus), receives the name of the articular piece of the jaw. The rest of Meckel's cartilage disappears.

Thus the primitive composition of the mandibular cartilaginous arch is the same in the bird as in the mammal ; in each, the arch becomes subdivided into an incudal and a Meckelian portion ; in each, the incudal and the adjacent extremity of the Meckelian cartilage, ossify, while the rest of the cartilaginous arch disappears and is replaced by a bony ramus deposited round it. But from this point the mammal and the bird diverge. In the former, the incudal and Meckelian elements are so completely applied to the purposes of the organ of hearing, that they are no longer capable of supporting the ramus, which eventually comes into contact with the squamosal bone. In the latter, they only subserve audition so far as they help to support the tympanic membrane, their predominant function being the support of the jaw.

The tympanic bone of every mammal is, at first, a flat, thin, curved plate of osseous matter, which appears on the outer side of the proximal end of Meckel's cartilage, but is as completely independent of it as is the ramus of the jaw of the rest of that cartilage. In most birds it has no bony representative.[1]

It is clear, then, as Professor Goodsir[2] has particularly stated, that the os quadratum of the bird is the homologue of the incus of the mammal, and has nothing to do with the tympanic bone ; while the apparently missing malleus of the mammal is to be found in the os articulare of the lower jaw of the bird.

It would lead me too far were I to pursue the comparison of the bird's skull with that of the mammal further. But sufficient has been said, I trust, to prove that, so far as the cranium proper is concerned, there is the most wonderful harmony in the structure of the two, not a part existing in the one which is not readily discoverable in the same position, and performing the same essential functions, in the other. I have the more willingly occupied a considerable time in the demonstration of this great fact, because it must be universally admitted that the bones which I have termed petrous, squamosal, mastoid, quadratum, articulare in the bird, are the homologues of particular bones in other oviparous *Vertebrata*, and consequently, if

[1] See Note III.

[2] Reichert, however, had already clearly declared this important homology in his 'Entwickelungsgeschichte des Kopfes,' p. 195.

these determinations are correct in the bird, their extension to the other *Ovipara* is a logical necessity. But the determination of these bones throughout the vertebrate series is the keystone of every theory of the skull—it is the point upon which all further reasoning must turn; and therefore it is to them, in considering the skulls of the other *Ovipara*, that I shall more particularly confine myself.

Composition of the Skull of the Turtle.

It has been seen that in birds the presphenoid, ethmoid, and orbitosphenoid regions are subject to singular irregularities in the mode and extent of their ossification. In the turtle, not only are the parts of the cranium which correspond with these bones unossified,

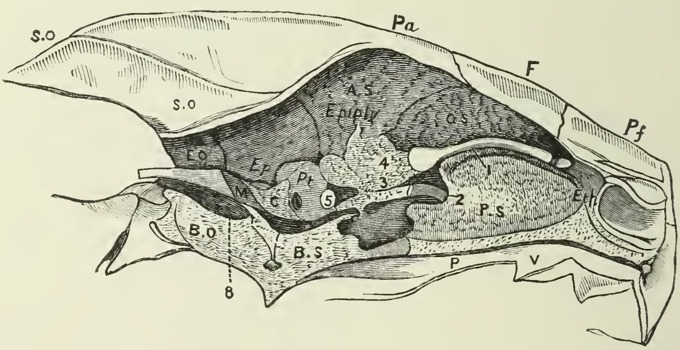


Fig. 5.—Longitudinal section of the Skull ot a Turtle (*Chelone mydas*), exhibiting the relations of the brain to the cranial walls. The dotted parts marked AS. OS. PS. and Eth. are cartilaginous.

but its walls remain cartilaginous for a still greater extent. In fact, if a vertical section be made through the longitudinal axis of a turtle's skull, it will be observed that a comparatively small extent of the cranial wall, visible from within, is formed by bone, and that the large anterior moiety is entirely cartilaginous and unossified. The anterior part of the posterior, bony, moiety of the cranial wall is formed by a bone (Pt.), whose long, vertical, anterior-inferior margin forms the posterior boundary of the foramen by which the third division of the trigeminal nerve makes its exit from the skull. The anterior and superior margin of the bone is very short, and articulates with the parietal bone. The superior margin is inclined backwards, and articulates with the supraoccipital. The posterior margin is straight, and abuts against a cartilaginous plate interposed between

this bone and that which succeeds it. The inner face of the bone is, as it were, cut short and replaced by this cartilage, whence the inferior edge is also short and is connected only with the basisphenoid, and not with the basioccipital. The anterior margin of the bone corresponds with the middle of the mesencephalon, while its inner face presents apertures for the portio dura and portio mollis. The posterior margin of its outer face forms half the circumference of the fenestra ovalis, and it contains the anterior and inferior portions of the labyrinth. Thus, with the exception of the absence of an inferior connexion with the basioccipital,—a circumstance fully explained by the persistence in a cartilaginous state of part of the bone, —it corresponds in the closest manner with the petrosal of the bird. I confess I cannot comprehend how those who admit the homology of the bone called petrosal in the bird with that called petrosal in the mammal (as all anatomists do), can deny that the bone in question is also the petrosal, and affirm it to be an alisphenoid. The general adoption of such a view would, I do not hesitate to say, throw the Theory of the Skull into a state of hopeless confusion, and render a consistent terminology impossible. Where then is the alisphenoid? I reply, that it is unossified. The posterior portion of the cartilaginous side-wall of the skull, in fact, unites with the parietal, the petrosal, and the basisphenoid, just in the same way as the bony alisphenoid of the bird unites with those bones. Furthermore, as in the bird, it bounds the foramen for the third division of the trigeminal nerve anteriorly, and is specially perforated by the second division of the fifth, while the optic and the other divisions of the fifth pass out in front of or through its anterior margin.

Not only is the alisphenoid cartilaginous, but the orbitosphenoid is in the same condition, and a great vertical plate of cartilage represents the whole anterior part of the craniofacial axis, or the presphenoid and ethmovomerine bones.[1] It has been imagined, indeed, that the rostrum-like termination of the basisphenoid represents the presphenoid, but I think this comes of studying dry skulls. Those who compare a section of the fresh skull of a turtle with the like section of the skull of a lamb, will hardly fail to admit that the rostrum of the basisphenoid in the turtle is exactly represented by that part of the sheep's basisphenoid, which forms the anterior and inferior boundary of the sella turcica, and that the suture between the basisphenoid and the presphenoid in the sheep corresponds

[1] Compare Kölliker's account of the primordial skull of a young turtle in the 'Bericht von der Königl. Zool. Anstalt zu Würzburg,' 1849.

precisely with the line of junction between the rostrum of the basisphenoid and the presphenoidal cartilage in the turtle.

Connected with the posterior edge of the petrosal by the cartilaginous plate, which has been referred to above, and between this and the exoccipital, there appears, on the inner aspect of the longitudinal section of the turtle's skull, a narrow plate of bone connected above, with the supraoccipital, behind, with the exoccipital, below, with the basioccipital, and leaving between its posterior margin and the exoccipital an aperture whereby the par vagum leaves the skull. In fact, except in being separated from the petrosal by cartilage, this bone presents all the characters of the mastoid of the bird, which it further resembles in forming one-half of the circumference of the fenestra ovalis. In other respects it is more like the mastoid of the sheep, for it is not anchylosed with the exoccipital ; it is produced externally into a great bony apophysis, which gives attachment to the representative of the digastric muscle ; and it is largely visible external to the exoccipital, when the skull is viewed from behind. Indeed, the resemblance to the mastoid of the mammal is more striking than that to the corresponding bone in the bird. And I think it is hardly possible for any unprejudiced person to rise from the comparison of the chelonian skull with that of the mammal, with any doubt on his mind as to the homology of the two bones.

When the sheep's skull is viewed from behind, the posterior half of the squamosal is seen entering into its outer boundary above the mastoid. On regarding the turtle's skull in the same way, there is seen, occupying the same position, the bone which Cuvier, as I venture to think, most unfortunately, named "mastoid." But if the arguments brought forward above be, as I believe with Hallmann, they are, irrefragable, this bone cannot be the mastoid ; and I can discover no valid reason why it should not be regarded as what its position and relations naturally suggest it to be—the squamosal. Its connections with the mastoid, petrosal, and quadratum are essentially the same as those of the squamosal in the bird and the mammal. The quadratum and articulare of the turtle are on all hands admitted to be the homologues of the similarly-named bones in the bird, and therefore all the reasonings which applied to the one apply to the other. When the petrosal, mastoid, and squamosal are determined in the turtle, they are determined in all the *Reptilia*. But the *Crocodilia*, *Lacertilia*, and *Ophidia* differ from the turtle and *Chelonia* generally, in that their mastoid is, as in the bird, anchylosed with the exoccipital. The squamosal, again, which in the *Crocodilia* essentially resembles that of the turtle, becomes a slender and elon-

gated bone in the *Lacertilia*, and still more in the *Ophidia*, in which the quadratum is carried at its extremity.[1]

In the *Amphibia* the petrous and mastoid have the same relations as in the *Reptilia* ; but it is interesting to remark, that in some *Amphibia* the anterior margins of the petrosal encroach upon the lateral walls of the skull so as completely to enclose the exit of the trigeminal, just as the posterior margin of the alisphenoid encroached so as to inclose it, in the sheep. It can be hardly necessary to remark, however, that this result has nothing to do with the disappearance of any element in the postero-lateral cranial walls, which have the same composition in the frog as in the crocodile or lizard.

The determination of the homologues of the squamosal, incudal, Meckelian, and tympanic elements in the amphibian skull is by no means an easy matter, but one requiring a much more careful investigation than it has yet received.

In *Mammalia*, a second arch, the hyoid, is connected with the outer surface of the skull, immediately behind the mandibular, and more particularly with that of the mastoid bone or its rudiment. The proximal end of this arch (which is, at first, like the mandibular arcade, a simple cartilaginous rod), in fact, usually becomes continuously ossified with the mastoid, forming part of the walls of the styloid canal ; while below this, and external to the tympanum, it is converted into that slender bone, which is known as the styloid process.

In adult birds and most reptiles, the upper end of the hyoid arch is free, but in some *Reptilia*[2] it is attached by a styloid process to the representative of the mastoid. Whether attached to the cranium or not, in all abranchiate *Vertebrata* the proximal end of the hyoidean arch is quite distinct from that of the mandibular arch.

In the *Amphibia*, however, I find a condition of the proximal ends of these two arches, which seems to foreshadow that intimate connexion between them which obtains in fishes. On the outer side of the petrosal, and of that part of the exoccipital which represents the mastoid, there lies a cartilaginous mass, which is continued downwards into a pedicle, with whose lower end the mandible is articulated. From the anterior edge of the proximal half of this pedicle, the narrow cartilaginous basis of the pterygoid passes forwards and

[1] See for the manner in which this is brought about, Rathke's 'Entwick. d. Natter.' Rathke, it should be said, regards this bone as the *tympanicum*, but its primitive place and mode of origin are those of the squamosal of the mammal.

[2] See Cuvier, 'Ossemens Fossiles,' x. p. 65 ; and Stannius, 'Zootomie der Amphibien,' p. 68.

upwards, to become directly continuous with the palatine bone in the frog, but to stop short of that point in the newt. Posteriorly, close to its proximal end, the pedicle becomes connected by a slender, fibrous or fibro-cartilaginous ligament with the upper extremity of the cornu of the hyoid. The hyoid and the mandibular arches are thus suspended to the skull by a common peduncle, which, to avoid all theoretical suggestion, I will simply term the "suspensorium."

The extent of the ossification which takes place, in and about this primitively cartilaginous suspensorium, varies greatly in different genera of *Amphibia*. Sometimes its distal end remains wholly unossified; sometimes, as in the common frog, a small outer portion of its lower extremity is ossified and sends a process forwards, becoming what is termed the quadratojugal bone; sometimes, as in the *Triton*, the distal half of the cartilage becomes more or less completely enclosed in a bony mass.

Another ossific deposit usually takes place in the outer half of the proximal end of the suspensorium, extending for a greater or less distance down towards the distal end, which it may even completely reach. It may be a simple triangular plate, as in *Triton*, or a T-shaped bone, as in *Rana*. In either case its lower end is the narrower, and fits into a kind of groove in the posterior and outer margin of the distal ossification.

This bone was considered by Cuvier to be the equivalent of the tympanic and the temporal (=squamosal); by Dugès it was called "temporomastoid."

The last constituent of this region of the skull in the *Amphibia* is one which is frequently overlooked altogether. In the frog, the membrana tympani is supported by a well-defined cartilaginous and partially ossified hoop, which is originally quite distinct from any of the elements of the suspensorium which have just been described, and which clearly deprives any of them of the right of being considered the homologue of the "tympanicum" of *Mammalia*.

I must defer the attempt to decide what the parts of the suspensorium really are, until the Piscine skull has been under consideration.

Composition of the Skull of the Carp.

The skulls of fishes present difficulties which necessitate, even for my present limited purpose, the entering into greater detail regarding them, than respecting those of the *Reptilia* or *Amphibia*. I select the cranium of the carp for description, as it departs far less widely

from the common plan, and therefore forms a better type for comparison with the skulls of other *Vertebrata* than that of any acanthopterygian or ganoid fish.

The craniofacial axis presents only four distinguishable bones. Behind, is the short basioccipital, with its cup for articulation with the first vertebra of the spinal column. In front of this is a greatly elongated bone, which, as in the bird, sends a process as far as the vomer, and forms the greater part of the axis of the skull; and which, I believe, represents, as in the bird, the basisphenoid and more or less of the presphenoid. The short vomer terminates the craniofacial axis anteriorly, and bears upon its upper surface a vertical septum, which, as in the bird, expands into a broad plate above, and is the ethmoid.

The orbitosphenoids, united below, spring from the upper and anterior part of the presphenoid. Behind them the lateral walls of

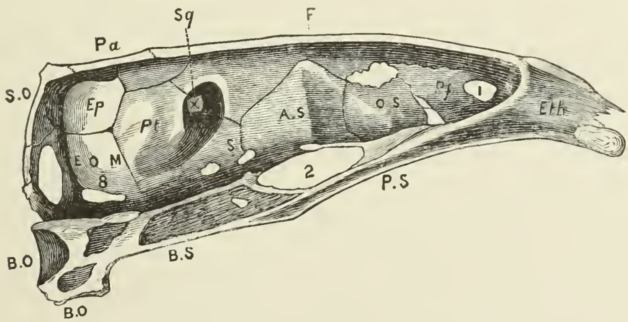


Fig. 6.—Longitudinal section of the Skull of a Carp (*Cyprinus carpio*).

the skull are formed by the alisphenoid. These bones have the same essential relations as in the bird, for the olfactory nerves pass out of the skull over, and in front of, the orbito-sphenoids; the optic nerves make their exit behind and beneath these and the alisphenoid, while the trigeminal makes its exit behind the posterior edge of the alisphenoid. When viewed from within, the foramen ovale is seen to be as in the bird, a mere conjugational foramen between the alisphenoid and the bone which follows it; and on an external view, the third division of the trigeminal is seen to pass entirely in front of the last-named bone.

The minutest scrutiny of the relations of this bone only strengthens the conviction suggested by the first view of it, that it is the homologue of the petrosal of birds, and therefore of mammals and reptiles. As in the bird, the anterior margin of the fish's petrosal is divided into a superior and an inferior portion, which meets at an angle,

the superior portion articulating with the parietal (and squamosal), the inferior with the alisphenoid. Inferiorly, the petrous articulates with the basisphenoid, and, to a small extent, with the basioccipital. Posteriorly it articulates with a bone through which the pneumogastric passes, and which, guided by the analogy of most *Reptilia*, of *Amphibia*, and of birds, I believe to represent the coalesced or connate mastoid and exoccipital. The bone lodges the anterior part of the auditory labyrinth ; its middle region corresponds with the middle of the mesencephalon. But as it does not separate the auditory organ from the cavity of the skull, it naturally presents no foramina corresponding with those through which the portio dura and portio mollis pass in Abranchiate *Vertebrata* and *Amphibia*. There is one relation of the petrosal in the fish, however, in which it seems to differ from that of any of the oviparous *Vertebrata* hitherto described. Superiorly and posteriorly, in fact, it does not unite with the supraoccipital, which is small, comparatively insignificant, and occupies the middle of the posterior and superior region of the skull ; but with a large and distinct bone which forms the internal of the two posterolateral angles of the skull, unites internally with the supraoccipital, anteriorly with the parietal and petrosal, inferiorly with the conjoined mastoid and exoccipital. It is the bone which was called "occipital externe" by Cuvier ; and he and others have supposed it to be the homologue of that bone in the turtle which, following Hallmann, I have endeavoured to prove to be the mastoid. As I have already shown, the true mastoid of the fish must be sought elsewhere, and consequently the Cuvierian determination is inadmissible. And I must confess, that if our comparisons be confined to adult *Vertebrata*, the only conclusion which can be arrived at seems to be, that this bone is peculiar to fishes.

But a remarkable and interesting observation of Rathke, combined with the peculiar structure of the skull of the chick described above, leads me to believe that when their development is fully worked out, we shall find a distinct representative of this bone in many, if not all, vertebrate crania.

In his account of the development of *Coluber natrix* (see Note IV.), Rathke states that three centres of ossification make their appearance in that part of the cartilaginous wall of the cranium which immediately surrounds the auditory labyrinth. One of these is anterior, and becomes the petrosal ; one is posterior, and eventually unites with the exoccipital ; the third is superior, and in the end coalesces with the supraoccipital. The posterior ossification clearly

represents the mastoid, and it is most interesting to find it, in this early condition, as distinct as in the Chelonian.

The superior ossification has only to increase in size and remain distinct in the same way as the mastoid of the turtle remains distinct, to occupy the precise position of the "occipital externe" of the fish. But, further, it is most important to remark, that when this primarily distinct bone has coalesced with the supraoccipital, it stands in just the same relation to that bone, to the petrosal, to the mastoid and to the semicircular canals, in the snake, as that lateral element, early confluent or connate with the supraoccipital in the chick, which I have termed the "os epioticum." I believe, then, that this "os epioticum," distinct in the young snake, but afterwards confluent with the supraoccipital, and becoming what may be termed the epiotic ala of that bone in the adult, is the homologue of the corresponding bone, or confluent ala of the supraoccipital, in birds and reptiles, while in the fish it remains distinct, and constitutes the "occipital externe."

For the rest, the superior part of the cranial arch in the carp resembles that of the bird. There are a supraoccipital, two parietals, and two frontals; the squamosal occupies the same position as in the chick, and as in the latter, is, in the dry skull, visible from within, in front of the petrosal.

As in the *Amphibia*, both the mandibular and the hyoidean arches are suspended by a pedicle or suspensorium, which is, to a certain extent, common to both, and presents a complexity of structure which can only be elucidated by the most careful study of development.

In ordinary fishes, such as the carp, stickleback, &c., the proximal end of the suspensorium is constituted by a single bone, Cuvier's "*temporal*," whose cranial end abuts against the squamosal, petrosal, and post-frontal bones.

This *temporal*[1] gives off posteriorly a process to which the cornu of the hyoid arch is attached; anteriorly and distally it ends in an expanded plate, with which two bones are connected, in front the *tympanal*, behind the *symplectique*. The distal end of the suspensor is constituted by the triangular *jugal*, whose distal and narrower extremity furnishes the condyle with which the mandib'e is articulated.

The elongated styliform *symplectique* is received into a groove on the posterior part of the inner surface of the *jugal*, and extends nearly to the condyle. In front, the jugal articulates with the *transverse*,

[1] In adopting the universally known Cuvierian appellations, I merely desire to avoid for the present all theoretical suggestions.

and more or less with the *pterygoidien*, which again are anteriorly connected with the *palatine*. The flat *tympanal* is fitted in between the *pterygoidien*, *jugal*, and *temporal*.

Besides these numerous bones, there are four others which enter less directly into the composition of the suspensorium. These are the *pre-opercule*, a sort of splint-like bone which lies on the outer and posterior faces of the *temporal* and *jugal*, and binds the two together; the *opercule*, which articulates with a special condyle developed for it from the posterior edge of the *temporal*, above the attachment of the hyoid; the *sousopercule*, which lies in the opercular membrane beneath this; and lastly, the *interopercule*, the

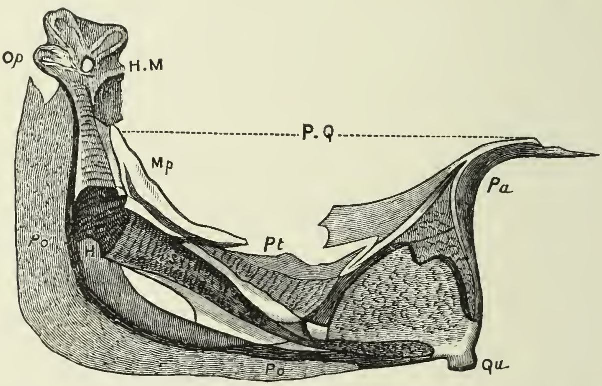


Fig. 7.—Palatosuspensorial arch of *Gasterosteus* from the inner side. HM. Hyomandibular bone. Op. Its articular facet for the operculum. Po. Pre-operculum. H. Articular surface for the styloid bone. Sy. Symplectic. P.Q. Palatoquadrate arch. Pa. Palatine bone. Qu. Quadratum. Pt. Pterygoid. Mp. Metapterygoid.

lowest of all, and commonly more or less closely connected with the angle of the lower jaw.

On examining the region in which these bones are eventually found, in an embryonic fish, I discovered, in their place, a delicate inverted cartilaginous arch, attached anteriorly, by a very slender pedicle, to the angles of the ethmoidal cartilage, and posteriorly connected by a much thicker crus with the anterior portion of that part of the cranial wall which encloses the auditory organ (fig. 8).

The crown of the inverted arch exhibits an articular condyle for the cartilaginous rudiment of the mandible. The posterior crus is not, as it appears at first, a single continuous mass, but is composed of two perfectly distinct pieces of cartilage applied together by their edges. The anterior of these juxtaposed pieces is continuous below

with the condyle-bearing crown of the arch, and with its anterior crus or pedicle (P.Q.). It is inclined backwards and upwards, and terminates close to the base of the skull in a free pointed extremity.

The posterior piece (S.Y.H.M.), on the other hand, has its broad and narrow ends turned in the opposite direction. Distally, or below, it is a slender cylindrical rod terminating in a rounded free extremity behind, but close to, the condyle for the mandible; above, it gradually widens and becomes connected with the cranial walls. On its posterior edge there is a convexity which articulates with the rudimentary operculum, and below this it gives off a short styloid process, to which the cartilaginous cornu of the hyoid is articulated. Thus the cartilaginous arch, which stretches from the auditory capsule to the ethmo-presphenoidal cartilage, consists, in reality, of two perfectly distinct and separate portions—the anterior division V-shaped, having its anterior crus fixed and its posterior crus free above; the posterior, styliform, parallel with the posterior leg of the V and free below. The anterior division supports the mandibular cartilage, the posterior the hyoidean cornu.

As ossification takes place, that part of the anterior crus of the V-shaped cartilage which is attached to the ethmo-presphenoidal cartilage becomes the *palatine*; its angle becomes the *jugal*; between these two the *transverse* and *pterygoidien* (represented by only one bone in *Gasterosteus*) are developed in and around the anterior crus: the *tympanal* arises in the same way around the free end of the posterior crus. Thus these bones constitute an assemblage which is at first quite distinct from the other elements of the suspensorium, and immediately supports the mandibular cartilage.

The proximal end (H.M.) of the posterior styliform division gradually becomes articulated with the cranial walls, and, ossifying, is converted into the *temporal*. The distal cylindrical end (S.Y.) becomes surrounded by an osseous sheath, which at first leaves its distal end unenclosed. The bone thus formed is the *symplectique*, which is at first free, but eventually becomes enclosed within a sheath furnished to it by the *jugal*, and so strengthens the union of the two divisions of the arch already established by the junction of the *tympanal* with the *temporal*. The *symplectique* and *temporal* do not meet, but leave between them a cartilaginous space, whence the supporting pedicle of the hyoid, which ossifies and becomes the *osselet styloide*, arises.

The operculum, suboperculum, interoperculum, and preoperculum are not developed from the primitive cartilaginous arch, but make

their appearance as osseous deposits in the branchiostegal membrane, behind, and on the outer side of, the posterior crus.

If we turn to the higher *Vertebrata*, we find, as I have stated above, that, at an early period of their embryonic existence, they also present a cartilaginous arch, stretching from the ethmo-presphenoidal cartilage to the auditory capsule, and supporting the mandibular or Meckelian cartilage on the condyle furnished by its inverted crown. The anterior part of the anterior crus of this arch becomes the palatine bone, which is therefore truly the homologue of the fishes'

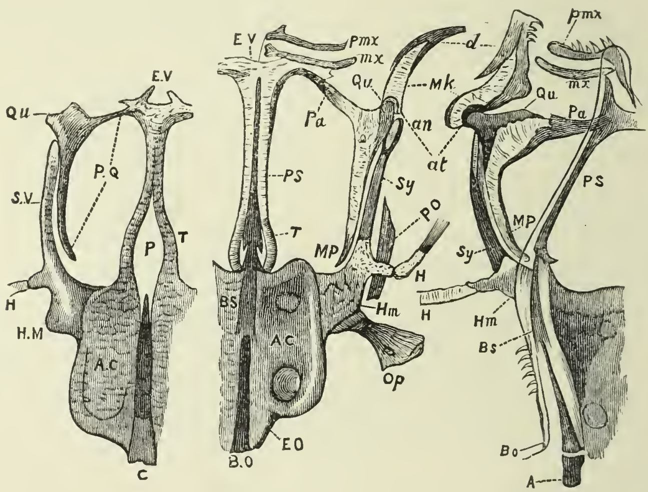


Fig. 8.—Cranium and face of young *Gasterostei* at different ages. The left-hand figure is a view of the base of the skull of a very young fish. The middle figure represents the under aspect, and the right-hand figure, a side view of a longitudinal section, of a more advanced stickleback's skull.

C. Notochord. P. Pituitary space. AC. Auditory capsules. T. Trabeculæ cranii. E.V. Ethmovomerine cartilage. P.Q. Palatoquadrate arch. Qu. Quadratum. S.Y. or Sy. Symplectic. H. Hyoidean arc. H.M. Hyomandibular cartilage. The other letters have the same signification as in the preceding figures, except *pmx*. Premaxilla. *mx*. Maxilla. *d*. Dentale. *an*. Angulare. *at*. Articulare. M*k*. Meckel's cartilage.

palatine. The posterior part of it becomes the pterygoid, which therefore is the homologue of the *pterygoïdien* (and *transverse*?) of the fish.

The produced crown of the arch in the higher *Vertebrata* becomes either the incus, or its equivalent, the quadratum. I therefore entertain no doubt that the *jugal* is really the homologue of the quadratum of other oviparous *Vertebrata*. That the *tympanal* has no relation whatsoever with the bone of the same name in the

higher *Vertebrata* is indubitable ; and I am unable to discover among them any representative of it. It seems to me to be an essentially piscine bone, to be regarded either as a dismemberment of the quadratum or of the pterygoid. It may be termed the " metapterygoid."

Still less do I find among the higher *Vertebrata* in their adult state, any representative of the posterior division of the suspensor, constituted by the *temporal* and *symplectique*. It is quite clear, that the *temporal* is not, as Cuvier's name would indicate, the homologue of the squamosal. The whole course of its development would negative such an idea, even if we had not a squamosal already ; and I shall therefore henceforward term it, from its function of affording support to both the hyoid and mandibular arches, the hyomandibular bone, " os hyomandibulare," while the other bone of this division may well retain the name of symplectic.

It is commonly supposed that the hyomandibular, symplectic, metapterygoid, and quadrate are all to be regarded as mere subdivisions of the quadratum of higher *Vertebrata*. Such a view, however; completely ignores and fails to explain, the connexion of the hyoidean arch with the hyomandibular bone. In no one of the higher *Vertebrata* does such a connexion ever obtain between any part of the quadratum and the hyoid, which are quite distinct, and attached separately to the walls of the cranium, in even young embryos of the abranchiate *Vertebrata*.

Nevertheless, in their very earliest conditions, these embryos are said to present a structure, which, if I mistake not, shadows forth the organization of the fish. The visceral arches, in which the mandibular and hyoid cartilages are developed, are at first separated to the very base of the cranium by a deep cleft, the anterior visceral cleft, so that the semi-cartilaginous rudiments of the mandibular and hyoid are completely separate. Subsequently they are said to coalesce above, as the visceral cleft diminishes, so as to have a common root of attachment to the cranium ; and this, I apprehend, answers to the hyomandibular bone, and its prolongation to the symplectic. With advancing development, however, this part does not advance, but remains stationary, and becomes confounded with the wall of the cranium ; so that the two arches subsequently appear to be attached to the latter quite independently, and there is nothing left to represent this division of the suspensorium in fishes.

I am strengthened in this view by the structure and development of the palatosuspensorial apparatus in the *Amphibia*, whose consideration I deferred when speaking of the skull in that class.

On examining a young tadpole (fig. 9), a cartilaginous process is seen to arise from the walls of the cranium, opposite the anterior part of the auditory capsule, and, passing obliquely downwards and forwards, to end in a rounded condyloid head, which articulates with the representative of Meckel's cartilage. At the anterior boundary of the orbit the process gives off a broad, nearly vertical apophysis (O), which ends superiorly in a free, rounded, and incurved edge. The

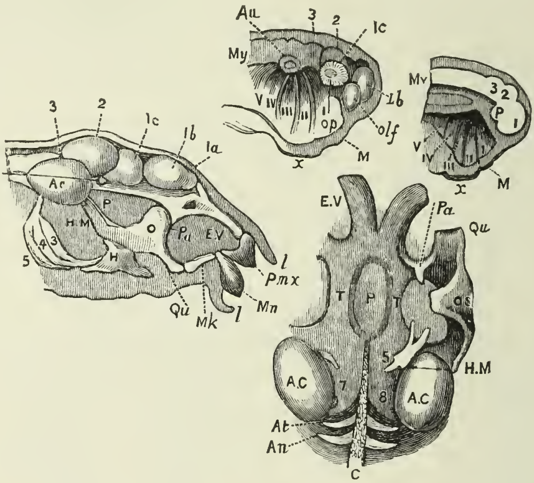


Fig. 9.—The upper right-hand figure represents a longitudinal section of the head of a Tadpole just about to be hatched. The upper left-hand figure exhibits a dissection of the head of a tadpole with external gills. The two lower figures represent dissections of the crania of tadpoles with well-developed hinder limbs. In the one, the integuments, organs of sense, &c. of the right side are taken away so as to lay bare the facial cartilages and the brain. In the other the cranium is opened from above, and the brain and myelon are extracted.

The letters have the same signification as before, except My. Myelon. M. Mouth. *olf.* Olfactory sac. *op.* Eye. 1. Anterior cerebral vesicle. 2. Middle cerebral vesicle. 3. Posterior cerebral vesicle. 1*a.* Rhinencephalon. 1*b.* Prosencephalon. 1*c.* Deutencephalon, or vesicle of the third ventricle. I. II. III. IV. V. Branchial arches. *x.* Organs of adhesion. l. Lips. 5. Trigeminal ganglion. 7. Ganglion of the portio dura. 8. Aperture for the exit of the pneumogastric.

crotaphite muscle passes to its insertion on the inner side of this, the so-called " orbitar process." From the condyle the cartilaginous process sweeps upwards and inwards, and ends by passing into the ethmo-presphenoidal cartilage. It consequently forms an inverted arch, whose keystone is the condyle for Meckel's cartilage, and is, in its connexions and form, strictly comparable with the cartilaginous arch which I have described in the embryo fish. The posterior crus

of the arch, it is true, is not divided into two parts, but nevertheless it represents the whole suspensorium of the fish, and not merely the quadratum of the abranchiate vertebrate, because immediately behind the orbitar process it presents an excavated surface, which articulates with the proximal end of the cornu of the hyoid. That part of the cartilaginous arch, therefore, which lies above and behind this point, corresponds with the proximal division of the suspensorium in the fish, or with the hyomandibular bone; while that portion which lies below and in front of it, corresponds with the distal division of the suspensorium and the anterior crus of the arch in the fish, or in other words, with the symplectic, quadratum, metapterygoid, pterygoid, transverse, and palatine bones.

In the course of development, in fact, the palatine bone appears, as in the fish, in that part of the arch which is immediately connected with the ethmo-presphenoidal cartilage, and a single pterygoid in that part of its anterior crus which lies between the palatine and the articular portion, which obviously represents the quadratum. But this pterygoid is, in the adult frog, a large bone, which, on the one hand, stretches down on the inner side of the quadrate cartilage, and, on the other, sends a process inwards and upwards, which nearly reaches the base of the skull. If the pterygoid, transverse, and metapterygoid of the fish were anchylosed into one bone, or if the corresponding region of the primitive cartilage were continuously ossified, the result would be a bone perfectly similar to the pterygoid of the frog; and I entertain no doubt that the amphibian pterygoid does really represent these bones.

The inferior ossification in the batrachian suspensorium certainly answers to the quadratum, in *Triton*—whether it should be regarded partly or wholly as a quadrato-jugale in the frog seems to be a question of no great moment—inasmuch as we may be quite sure that the lower end of the frog's suspensorium represents the quadrate or incudal element in other *Vertebrata*.

It is well known that, in the course of the development of the frog, the end of the suspensorium, as it were, travels backwards, so that its axis, instead of forming an acute angle, open forwards, with that of the cranium, as in the tadpole (fig. 9), forms a very obtuse angle, open downwards, in the adult frog. This change is accompanied by a relative and absolute lengthening of that part of the suspensorium which lies between the articulation of the hyoid and that of Meckel's cartilage (containing its proper quadrate portion), and by a relative shortening of that part which lies between the articulation of the hyoid and the skull (or the hyomandibular portion). The conse-

quence of this is, that the articular surface for the hyoid appears constantly to approach the cranial wall, until at length, in the adult, it seems to be almost in contact with it. If a knife were passed obliquely between the pterygoid and the suspensorium, and then carried through the suspensorium to its posterior margin a little above the condyle for the mandible, it would divide the suspensor into a proximal and a distal portion, precisely resembling those which naturally exist in the embryonic fish. If the proximal division ossified, it would clearly represent the hyomandibular and symplectic bones. Now in the *Amphibia*, although the suspensor is not thus divided, it ossifies very nearly as if it were, and the superior or proximal ossification is the so-called "temporo-tympanic," "temporo-mastoid," or "squamosal" bone.[1]

That this bone is really the homologue of the hyomandibular and symplectic in the fish, becomes, I think, still more clear when we compare it with such an aberrant form of piscine suspensorium as is presented by some of the eel-tribe (*Murœna*, *e.g.*). In these fishes the suspensorium is formed by only two bones, a small distal quadratum, which, as usual, articulates with the lower jaw, and a large wide proximal bone, which articulates above with the post-frontal and squamosal, gives attachment to the operculum and to the cornu of the hyoid, and sends down a process towards the articular head of the quadratum. The single bone, which represents the three pterygoids of other fishes, is articulated for the most part with the quadratum, but partly with this proximal bone. The latter, therefore, clearly represents both the hyomandibular and the symplectic bones of ordinary fishes.

But if the suspensorium of *Triton* be compared with that of *Murœna*, *e.g.*, it will, I think, be hardly doubted, that while the distal ossification in the former corresponds with the quadratum, the proximal answers (at any rate, chiefly) to the hyomandibular bone of the *Murœna*. Indeed it differs from the latter principally in being an ossific deposit in the outer portion only of the primitive cartilage.[2]

Thus it would seem, that in the manner in which the lower jaw is

[1] See this result, well worked out, by the method of gradation only, by Köstlin (*l. c.* pp. 328–332), who draws particular attention to the resemblance between the suspensorium of the *Amphibia* and that of fishes of the Eel-tribe.

[2] In *Murœna Helena* the suspensorium forms an obtuse angle with the axis of the skull, though not so obtuse as in the frog. A strong ligament connects the outer side of the distal end of the quadratum with the maxillary bone, passing outside the lower jaw. If the posterior end of the ligament were ossified, it would correspond very nearly with the "quadratojugal" of the frog.

connected with the cranium, *Pisces* and *Amphibia*, as in so many other particulars, agree with one another, and differ from *Reptilia* and *Aves* on the one hand, as much as they do from *Mammalia* on the other. And the difference consists mainly, as might be anticipated, in the large development in the branchiate *Vertebrata* of a structure which aborts in the abranchiate classes. A most interesting series of modifications, all tending to approximate the ramus of the mandible more closely to the skull,[1] is observable as we pass from the fish to the mammal. In the first, the two are separated by the hyomandibular, the quadrate, and the articular elements, the first of which becomes shortened in the *Amphibia*. In the oviparous abranchiate *Vertebrata* the cranium and the ramus are separated only by the quadratum and the articulare, the hyomandibulare having disappeared. Finally, in the mammal, the quadratum and the articulare are applied to new functions, and the ramus comes into direct contact with the cranium.

The operculum, suboperculum, and interoperculum appear to me to be specially piscine structures, having no unquestionable representatives in the higher *Vertebrata*. Much might be said in favour of the identification of the preoperculum with the tympanic bone; but there are many arguments on the other side, and at present I do not see my way to the formation of a definite conclusion on this subject.

In the preceding discussion of the structure of the osseous vertebrate skull, I have desired to direct your attention, more particularly, to the consideration of those fundamental bones, the determination of whose homologues throughout the vertebrate series is of the greatest importance for my present object. The presphenoid, ethmoid, mastoid, and petrosal are the Malakhoff and the Redan of the theory of the skull; and if anatomists were once agreed about their homologues, there would be comparatively little left to dispute about.

But besides the axial, inferolateral, and superior series of bones, there are other, less constant, elements of the cranial wall, forming a discontinuous superolateral series. These are the epiotic, the squamosal, the postfrontal, the prefrontal, and lacrymal bones. Of the two first-named of these bones I have already spoken sufficiently. The postfrontal exists only in Reptiles and Fishes, and is always situated between the frontal, alisphenoid, petrosal, and squamosal—

[1] Of course in a morphological sense. Whether they are more or less distant in actual space, is not the question.

the extent to which it is absolutely in contact with any one of these bones varying.

The prefrontal and lacrymal bones are always developed in or upon that lateral process of the ethmosphenoidal plate, which gives attachment externally to the palatopterygoid arch ; consequently they lie at the anterolateral ends of the frontal, and have more or less close relations with it, the ethmoid and the palatine bones.

Finally, the nasal bones (or bone) never enter into the composition of the walls of the skull, but have the same relation to the anterior and upper expanded edge of the prolonged lamina perpendicularis or body of the ethmoid, as the vomer or vomers have to its lower edge.

If the conclusions which I have laid before you are correct, the following propositions are true of all the bony skulls of *Vertebrata.*

1. Their axis contains at most five distinct bones, which are, from before backwards, the basioccipital, the basisphenoid, the presphenoid, the ethmoid, and the vomer ; but any of these bones, except the basisphenoid, may be represented by cartilage, and they may anchylose to an indefinite extent ; so that the number distinguishable as separate bones in any skull cannot be predicated. The craniofacial axis invariably presents the same regions, but the histological character of these regions may vary.

2. Their roof contains at most, leaving Wormian bones out of consideration, five bones (supraoccipital, parietals and frontals), or seven, if we include the epiotic bones in the roof. The number falls below this in particular cases, for the same reason as that given for the apparent variations in composition of the axis.

3. Their inferolateral wall contains at most six pair of bones (exoccipitals, mastoids, petrosals, alisphenoids, orbitosphenoids, prefrontals), whose apparent number, however, is affected by the same causes.

4. The axial bones have definite relations to the brain and nerves. The basioccipital lies behind the pituitary body, the basisphenoid beneath it, the presphenoid in front of it. In fact the pituitary body may be regarded as marking the organic centre, as it were, of the skull—its relations to the axial cranial bones being the same, as far as I am aware, in all *Vertebrata.*

The olfactory nerves pass on either side of the ethmoid, which bounds the cranial cavity in front, the greater part of its substance and that of the vomer being outside the cranial cavity.

5. The lateral bones have definite relations to the brain, nerves, and organs of sense. The exoccipital lies behind the exit of the par

vagum; the mastoid lies in front of it; the petrosal lies behind the exit of the third division of the trigeminal; the alisphenoid lies in front of it; though either bone may, to a certain slight extent, encroach on the province of the other. The optic nerve passes out more or less in front of the alisphenoid, and behind, or through, the orbitosphenoid.

The organ of hearing is always bounded in front by the petrosal bone, which limits the anterior moiety of the fenestra ovalis.

The organs of smell always lie on each side of the ethmovomerine part of the axis.

The greater part, or the whole, of the petrosal lies behind the centre of the mesencephalon.

6. The attachment of the mandibular arch to the skull is never situated further forward than the posterior boundary of the exit of the trigeminal; consequently it cannot belong to any segment of the skull in front of the petrosal.

But if propositions of this generality can be enunciated with regard to all bony vertebrate skulls, it is needless to seek for further evidence of their unity of plan. These propositions are the expression of that plan, and might, if one so pleased, be thrown into a diagrammatic form. There is no harm in calling such a convenient diagram the 'Archetype' of the skull, but I prefer to avoid a word whose connotation is so fundamentally opposed to the spirit of modern science.

Admitting, however, that a general unity of plan pervades the organization of the ossified skull, the important fact remains, that many vertebrated animals—all those fishes, in fact, which are known as *Elasmobranchii*, *Marsipobranchii*, *Pharyngobranchii*, and *Dipnoi*—have no bony skull at all, at least in the sense in which the words have hitherto been used. In these *Vertebrata* the skull is either membranous or cartilaginous; or if ossified, the ossific matter presents no regular grouping around a few distinct centres.

Thus the cranium of the *Amphioxus* is nothing but a membranous capsule, whose walls are continuous with those of the canal for the spinal cord, and in whose floor lies a continuation of the notochord which underlies the spinal canal.

In the *Marsipobranchii* there is a marked increase in the capacity of the cranium as compared with that of the spinal canal, in correspondence with the decided differentiation of the cerebral masses; and, at the same time, the cranial walls have undergone a more or less extensive chondrification. The notochord terminates in the midst of the firm and solid cartilaginous plate which forms the posterior part of the basis cranii, and which sends forward two processes, including

a membranous interspace. The auditory capsules are enclosed within prolongations of the sides of the basilar plate ; and just in front of and below them, the root of each process of the basal plate gives off a solid prolongation, which passes at first outwards and downwards, and then bends upwards and forwards, to rejoin the anterior part of the process of the basilar plate of its side. An inverted arch is thus formed, and the space included between its crura and the sides of the cranium, constitutes the floor of the orbit.

The posterior crus of the arch is divided into two, more or less distinct, pillars, the posterior of which supports the hyoidean arc ; the mandibular arc appears to be absent.

The apertures whereby the cranial nerves make their exit are situated in the side-walls of the capsule, that for the vagus lying immediately behind the auditory capsule, while that for the trigeminal is immediately in front of the same organ. The olfactory nerves perforate the anterior walls of the cranial capsule ; the optic, its lateral walls between them and the trigeminal.

The skulls of the *Elasmobranchii*, again, appear at first to be something quite different from either of these. The cranium is here a cartilaginous box, more or less incomplete and membranous above, and presenting on each side posteriorly a transverse enlargement, in which the auditory organ is contained ; while anteriorly it expands into a broad plate, which on each side overhangs the olfactory sacs. The notochord and the membranous space have disappeared, or their traces only are visible in the base of the cranium, whose walls are, as it were, crusted with a multitude of minute plates of bone.

In the *Chimæræ* the inferolateral walls of the cranium pass into a cartilaginous arch-like plate which form the floor of the orbit, and whose posterior part, as in the *Marsipobranchii*, gives attachment to the hyoidean arch ; besides which, a mandibular cartilage is connected with the condyloid surface developed from the crown of the arched plate.

In the Plagiostomes there is also an inverted suborbitar arch with a mandibular cartilage and a hyoidean apparatus, but the structure of the arch is different from what obtains in *Chimæræ*.

The outer wall of that portion of the cranium which lodges the auditory organ, in fact, furnishes an articular surface for a strong moveable peduncle, to which the hyoid arc is usually attached. At its lower end, however, this peduncle does not articulate with the mandibular cartilage, but is directly connected with a strong cartilaginous plate which forms the upper boundary of the gape, and is articulated anteriorly with the sides of the skull in front of the orbit

This plate bears the upper series of teeth, and bites more or less directly against the mandible, which is moveably articulated with a condyle furnished by its posterior extremity.

The upper plate is commonly, though, as I think, erroneously, regarded as the homologue of the maxilla and premaxilla in other fishes ; the peduncle as the homologue of their whole suspensorium.[1]

The par vagum leaves the skull behind the auditory organ ; the trigeminal passes out in front of it ; and then its third division traverses the space enclosed between the peduncle, the upper plate, and the skull. The optic nerve passes through the lateral walls of the skull in front of the trigeminal, and the olfactory perforates its anterior boundary.

So brief and simple a statement of the characters of the skulls of these three orders of fishes, while it brings their diversities into prominence, also exhibits an amount of uniformity among them which is not a little remarkable. The exits of the great nerves have fixed relations to the auditory capsules, to the anterior boundary of the skull, and to the pituitary body. The inferior arc of the hyoid is constant (except in the *Pharyngobranchii*), and has always, speaking broadly, the same relative position with respect to the auditory capsule and the posterior crus of the suborbitar arch. The suborbitar arch itself is always present (except in *Pharyngobranchii*) ; its posterior crus is always attached to the cranium behind the third division of the trigeminal nerve, while the anterior is invariably fixed to that part of the skull which lies behind, or beside, the base of the olfactory capsule.

Thus the employment of the method of gradation alone exhibits a surprising uniformity in the organization of these lower forms of skull ; and on comparing them with the higher forms, it seems obvious that, so far as it goes, their plan is identical with that of the latter ; for the relations of the auditory organ to the par vagum and trigeminal are the same in each ; the posterior crus of the suborbitar arch answers to the suspensorium of *Teleostei*, its anterior crus to their palatopterygoid apparatus. But with all this, there are discrepancies in the structure of the skull itself, which would forbid too close an approximation between the bony and the unossified crania, if their adult forms alone were examined. The study of the development of the ossified vertebrate skull, however, eliminates this difficulty, and satisfactorily proves that the adult crania of the lower *Vertebrata* are but special developments of conditions through which the embryonic crania of the highest members of the subkingdom pass.

[1] See Note IV., on the suspensorium in fishes.

It is to Rathke's luminous researches that we are indebted for the first, and indeed, even now, almost the only, demonstrative evidence of this great fact. Twenty years ago that great and laborious embryologist worked out the early stages of the development of the skull in each class of the *Vertebrata*. Confirmed and adopted by Vogt and Bischoff, his conclusions have been feebly controverted, but never confuted; and my own observations lead me to believe that they are destined to take a permanent place among the data of biological science. Nothing is easier than to verify Rathke's views in an embryonic fish or amphibian; and as it matters not which of the higher *Vertebrata* is selected for the study of cranial development, I will state at some length what I have observed in the embryonic frog.[1]

Before the dorsal laminæ have united so as to enclose the primitive craniospinal cavity, the anterior portion of the floor of that cavity is bent downwards. The angle which the deflexed portion forms with the rest becomes less and less obtuse, until, when the dorsal laminæ have united and the visceral clefts have begun to appear, it constitutes a right angle.

On examining the floor of the craniospinal cavity at this period, it is seen that the notochord, at present formed by the aggregation of a number of yelk segments or embryo-cells, small in themselves, but larger than those of which the rest of the body is composed, ends in a point immediately behind the angular flexure.

The notochord has no sheath as yet, and is not in any sense prolonged into the deflexed portion of the floor of the craniospinal cavity.

When the visceral clefts first appear, they are best seen from the inner or pharyngeal aspect of the visceral wall. Five, of which the two anterior are the longest and about equal, while the others gradually diminish in length from before backwards, can be distinctly observed. They mark out the boundaries of a corresponding number of "visceral arches," and there is sometimes an appearance as of a sixth visceral arch behind the last cleft. A horizontal section shows that these arches differ in nothing but their relative size—in no other respect can one of them be distinguished from the other.

The anterior visceral cleft lies in a transverse plane, immediately behind the angular bend of the floor of the craniospinal cavity, or, as I shall henceforward term it, mesocephalic flexure. Consequently the posterior part of the first visceral arch passes into the future basis cranii close to the flexure.

The parts of the cerebrum are now distinguishable. It is bent in

[1] See Note V. for the development of the skull in other *Vertebrata*.

correspondence with the mesocephalic flexure, and its most projecting portion, or the angle of the bend, is the rudiment of the mesencephalon. The large rudiment of the pituitary body lies immediately in front of the flexure, and is therefore altogether anterior to the end of the notochord and to the posterior part of the first visceral arch. The rudiment of the eye lies at first altogether in front of the flexure, and therefore anterior to the root of the first visceral arch.

The auditory vesicles make their appearance on each side of a line which would cut the chords a little behind its anterior termination. They are at first quite free and perfectly distinct from the walls of the cranium, which is in accordance with Remak's statement, that they are originally formed by the involution of the epidermic layer of the embryo. They long remain separate and easily detachable from the cranial walls.

Ten days after impregnation, larvæ with rudimentary external gills and colourless blood, still exhibited some traces of the mesocephalic flexure, but the angle formed by the anterior and posterior portions of the cranium was very obtuse ; the base of the cranium had, in fact, undergone a gradual straightening. The rudiments of the cranial skeleton had made their appearance, and consisted, behind the mesocephalic angle, of a broad semi-cartilaginous plate enclosing the anterior end of the notochord, but not covering it above or below. It is not as yet adherent to the auditory sacs.

That part of the middle of the basis cranii which underlies the pituitary body is not converted into cartilage, but remains membranous, and may be called the "subpituitary membrane." The delicacy of this membrane is so great that it is easily torn, when the pituitary body seems, as Rathke originally supposed, to unite with the palatine mucous membrane. But that this is not really the case, is readily demonstrable in an embryo whose tissues have been sufficiently hardened with alcohol or nitric acid.

The cartilaginous basal plate gives off a prolongation on either side of the subpituitary membrane. This, the "cranial trabecula" (Schädelbalke of Rathke), passes forwards with a slight convexity outwards, and then turning inwards comes into contact with its fellow (from which, however, it is at first distinct), and spreads out into a broad, flat, elongated process, which I shall term the ethmo-vomerine cartilage.

Behind the eye and just in front of the auditory capsule (in the posterior part of the first visceral arch, therefore), a cartilaginous process lies, which is connected proximally with the root of the

trabecula close to the basal plate, while at its distal end it sends a prolongation upwards to unite with the posterior end of the ethmovomerine cartilage. It then forms an arch, between which and the basis cranii is an interspace corresponding with, and lodging, the under surface of the large eyeball. The rudiments of the hyoid, mandibular and maxillary apparatus in larvæ at this stage are somewhat indistinct ; and indeed not only in this, but in other respects, more instruction is to be derived from tadpoles which have advanced further.

In larvæ, with completely internal branchiæ and very short tubercles in the place of hind limbs, the notochord suddenly narrows between the auditory capsules to hardly more than half its preceding dimensions, and then gradually tapers off, to what appears to be a rounded end, a short distance from the anterior boundary of the basal plate. On very careful examination, however, a delicate process (which may by possibility be nothing but a cavity in the cartilage) can be traced from it very nearly to the margin of the basal plate. But there is no continuation whatsoever, either of the notochord itself or of its sheath, into the subpituitary membrane, which is now composed of delicate connective tissue, and from its extreme thinness and transparency would exhibit the least trace of such a prolongation. And I speak the more confidently on this point, because the delicate process of the notochord or cavity in the cartilage, to which I have referred, contains opaque unchanged vitelline granules, and is therefore particularly conspicuous. The basal cartilage is still divided by the notochord into two lateral moieties, which are only united by a short band of cartilage in front of the end of the notochord. It sends off from its outer side a cartilaginous process, which envelopes the auditory capsule externally, but leaves on its inner side a wide aperture for the entrance of the auditory nerve. The oval auditory capsules thus formed have their long axis directed outwards and forwards.

The trabeculæ are still better developed than before, but instead of remaining distinct anteriorly, they have become fused together into a single trapezoidal cartilage, which may be termed the ethmopresphenoidal plate. This plate, as it were, divides anteriorly into two flat, elongated and somewhat divergent processes, which are concave downwards and end in truncate extremities. Fibrous tissue connects the ends of these ethmovomerine processes with a crescentic cartilaginous plate which supports the horny upper jaw of the tadpole

The posterior crus of the palatosuspensorial, or suborbitar, arch is

not yet united with that portion of the cranial wall which encloses the auditory capsule; but for the rest the same description applies to it which has already been given of the palatosuspensorial arch and its appendages in more advanced tadpoles. In this state, the roof, and all the lateral walls of the cranium, but that part into which the auditory capsule enters, are membranous.

If the skull of the larval frog just described, be laid open and the exit of the nerves observed (fig. 9), it will be seen that the par vagum makes its way out by a foramen situated immediately behind the auditory capsule; that the third division of the trigeminal leaves the cranium in front of the auditory capsule, passing over the posterior crus of the palatosuspensorial arch; and that the optic traverses the membranous walls of the skull between this and the olfactory nerve, which perforates the anterolateral region to enter the olfactory capsules. The latter are situated wide apart, on each side and in front of, the broad ethmo-presphenoidal cartilage and the anterior crus of the palatosuspensorial arch, and are even a little overlapped by the edges of the ethmovomerine processes.

In the further course of development, the trabeculæ approximate and elongate, so as to obliterate the subpituitary membrane, and form with the enlarged basal cartilage, the ethmoid cartilage and the ethmovomerine cartilages, the continuous cartilaginous craniofacial axis. A histological metamorphosis into cartilage is undergone by the roof of the occipital region of the skull, but in front of this it remains membranous; so that in the adult frog (in which this cartilaginous framework persists), the skull, when deprived of its bony matter, presents an anterior fontanelle. The ethmovomerine cartilages diverge still more, and form the broad mass whose lateral cavities shelter the olfactory sacs in the adult frog. If, bearing in mind the changes which are undergone by the palatosuspensorial apparatus, and which have already been described, we now compare the stages of development of the frog's skull with the persistent conditions of the skull in the *Amphioxus*, the Lamprey, and the Shark, we shall discover the model and type of the latter in the former. The skull of the *Amphioxus* presents a modification of that plan which is exhibited by the frog's skull, when its walls are still membranous and the notochord is not as yet embedded in cartilage. The skull of the lamprey is readily reducible to the same plan of structure as that which is exhibited by the tadpole, while its gills are still external and its blood colourless. And finally, the skull of the shark is at once intelligible when we have studied the cranium in further advanced larvæ, or its cartilaginous basis in the adult frog.

Thus, I conceive, the study of the mode in which the skulls of vertebrate animals are developed, demonstrates the great truth which is foreshadowed by a careful and comprehensive examination of the gradations of form which they present in their adult state ; namely that they are all constructed upon one plan ; that they differ, indeed, in the extent to which this plan is modified, but that all these modifications are foreshadowed in the series of conditions through which the skull of any one of the higher *Vertebrata* passes.

But if these conclusions be correct, the first problem which I proposed to you,—Are all vertebrate skulls constructed upon a common plan?—is solved affirmatively.

We have thus attained to a theory or general expression of the laws of structure of the skull. All vertebrate skulls are originally alike ; in all (save *Amphioxus*?) the base of the primitive cranium undergoes the mesocephalic flexure, behind which the notochord terminates, while immediately in front of it, the pituitary body is developed ; in all, the cartilaginous cranium has primarily the same structure,—a basal plate enveloping the end of the notochord and sending forth three processes, of which one is short and median, while the other two, the lateral trabeculæ, pass on each side of the space, on which the pituitary body rests, and unite in front of it ; in all, the mandibular arch is primarily attached behind the level of the pituitary space, and the auditory capsules are enveloped by a cartilaginous mass, continuous with the basal plate between them. The amount of further development to which the primary skull may attain varies, and no distinct ossifications at all may take place in it ; but when such ossification does occur, the same bones are developed in similar relations to the primitive cartilaginous skull. But the theory of the skull thus enunciated is not a 'vertebral theory' ; one may have a perfectly clear notion of the unity of organization of all skulls without thinking of vertebræ.

So much for the first problem before us. I now proceed to the second question, which was, you will recollect, Given the existence of a common plan of organization of all vertebrate skulls ; is this plan the same as that of a spinal column?

To deal properly with this question, we must know what is the plan of organization of a spinal column, and that can be learnt only by a careful study of its development, as well as of its adult modifications. Indeed, the latter are unintelligible without a knowledge of the former.

It is impossible to form a clear conception of the essential nature of the process of development of a spinal column, or to compare it

with that of the skull, unless we analyse very carefully, and distinguish from one another, the successive steps of that process.[1]

1. The primary changes of form exhibited by the blastoderm in the region of the spinal column, are, in all the *Vertebrata* whose development has yet been studied, precisely the same. Two ridges, the "laminæ dorsales," bounding a narrow elongated groove, rise up and eventually unite with one another so as to enclose a cavity—the neural canal. External to the junction of the laminæ dorsales with the blastoderm, the latter is converted more or less completely into the "laminæ ventrales," which become incurved, unite, and eventually enclose the visceral cavity.

A transverse section of the embryo in this state shows a very thin and narrow median plate, separating the neural canal above, from the hæmal or visceral canal below, and passing on each side into thickened masses of blastoderm, which give rise to the laminæ dorsales on the one hand, and to the laminæ ventrales on the other.

For convenience of description, I shall term the median plate the "diaphysial plate," and the lateral ridges the "paraphysial thickenings."

2. The primary histological differentiations, which take place in the rudimentary spinal column just described, are the same in all *Vertebrata*.

A long filament, composed of indifferent tissue, makes its appearance in the middle of the diaphysial plate, and constitutes the notochord, or chorda dorsalis.

Next, the substance of the paraphysial thickenings undergoes a certain change of tissue at regular intervals, so that they acquire a segmented appearance ; solid, broad, darker masses of blastema lying opposite one another in each paraphysial thickening, and being separated by clear, narrow interspaces.

These segments are what the Germans term "Urwirbel," or "primitive vertebræ ;" a somewhat misleading name, as they are in every way distinct from what are commonly understood under the name of "vertebræ," even if we use that word in its broadest signification. Professor Goodsir's terms of *Somatomes* for the segments and *Metasomatomes* for their interspaces, appear to me to be well worthy of adoption as the equivalents of these "Urwirbel."

3. The next step in the development of a vertebral column, is the histological differentiation of the somatomes. Leaving out of consideration the epithelial and other minor tissues, it may be said

[1] See Note VI. for the details of the development of the spinal column in *Vertebrata* generally.

that each somatome gives rise to (*a*) epiaxial muscles, (*b*) a nerve and its ganglion, (*c*) the blastema for a vertebral centrum and its neural and hæmal arches, and (*d*) possibly hypaxial muscles ; while the metasomatome becomes for the greater part of its extent an " intermuscular septum."

It is unnecessary for my present purpose to trace out particularly the development of any of these parts, except the centrum and its arches.

The blastema, which is specially intended for these parts, appears, in a distinct form, first, in the paraphysial thickenings, and then extends inwards above and below, so as gradually to enclose the notochord in a sheath, while, externally, it passes in the posterior half of each somatome, upwards into the neural arches, and downwards into the hæmal arches.

4. In some *Vertebrata* the spinal column never gets beyond this stage, nor even so far ; but for the present it will be well to confine our attention to those which become completely ossified. In these chondrification is the next step. The blastema of the centra and its prolongations becomes converted into cartilage, but not continuously. On the contrary, at points corresponding with the intervals between every pair of metasomatomes, or with the middle of each somatome, the cartilage is replaced by more or less fibrous tissue. As a consequence, the cartilaginous sheath of the notochord is now divided into regular segments, which alternate with the somatomes, so that each metasomatome abuts upon the middle of one of these cartilaginous vertebral centra.

In every centrum it is necessary to distinguish three tracts or regions :—1. A diaphysial region immediately surrounding the notochord. 2. Two paraphysial regions lying in the paraphysial thickenings. The paraphysial regions give rise to the cartilaginous neural and hæmal semi-arcs, which are primitively continuous with them ; so that all parts of the vertebra form one connected whole.

The neural semi-arcs eventually unite in the middle line, and ordinarily send a prolongation upwards from their junction. The hæmal semi-arcs also tend to unite below, but in a somewhat different manner.

5. The last step in the development of the vertebra is the differentiation of its various parts from one another, and their final metamorphosis into their adult form. The notochord, which primitively traversed the centra and the intercentra (intervertebral ligaments, synovial membranes, or the like, between the centra), becomes more or less completely obliterated.

The distal, larger part of the hæmal semi-arc is commonly distinguished from its proximal smaller part, by the conversion of its cartilage into osseous or other tissue, and thus the semi-arc becomes separated into a rib and an articular surface or process, for the head of that rib, to which last the term *Parapophysis* may be conveniently restricted.

In the dorsal vertebræ of many *Vertebrata*, the neural semi-arc sends out a process, the *Diapophysis*, which is eventually met by a corresponding outgrowth of the rib, its so-called tubercle, and the two become firmly connected together.

When ossification occurs, it is a very general, if not invariable rule, that an annular deposit around the notochord takes place in the centrum. I term this the *Diaphysis* of the vertebra. In some fishes a distinct centre of ossification appears in each paraphysial region, and this may be termed the *Paraphysis* of the vertebra.

In mammals each end of the vertebra ossifies from a distinct point, and constitutes a central *Epiphysis* of the vertebra; and in many *Vertebrata* a part of the under surface of a centrum ossifies separately as a distinct *Hypophysis*. It is another very general, if not invariable rule, that a distinct centre of ossification appears in, or on, each neural semi-arc or *Neurapophysis*, and passes upwards, into the spine or *Metaneurapophysis*; downwards, to unite sooner or later with the diaphysis, or diaphysis and paraphysis; and outwards into the diapophysis.

It is doubtful whether the paraphysis appears as a distinct osseous element in any *Vertebrata* above the class of fishes, in very few of which even, is it distinguishable in the adult state. Consequently in the higher *Vertebrata* the paraphysial region is ossified, either from the diaphysis or from the neurapophysis, or from both; and a suture exists for a longer or shorter time at the point of junction of the neural and central ossifications. I will term this the *Neurocentral suture*. Its position is no certain or constant indication of the nature of the parts above or below it, for it may vary in the same vertebral column from the base of the neurapophysis, to the junction of the paraphysial with the diaphysial region of the centrum.

The number of the centres of ossification in each distal portion of the hæmal semi-arc may vary greatly; the uppermost is called a *Pleurapophysis*, the lower, *Hæmapophyses* and *Met-hæmapophyses*.

Besides these primary centres of ossification of a vertebra, there are others of less constancy. Thus the ends of the metaneurapophyses, diapophyses, and zygapophyses in many *Mammalia* are ossified from distinct centres; and in the caudal region of many of the higher

Vertebrata, outgrowths of the centra unite below to enclose the caudal vessels, and ossify as distinct apophyses.

If the development of the skull be now compared with that of the spinal column, it is found that (1) the very earliest changes undergone by the blastoderm in each are almost identical. The primitive groove extends to the extremity of the future cranial cavity; its lateral walls are continuous with the laminæ dorsales, and these pass into laminæ ventrales, also continuous with those of the spinal region. The laminæ dorsales of the head become the cranial walls and enclose the cerebrum—the continuation of the myelon; the laminæ ventrales give rise to the boundaries of the future buccal and pharyngeal cavities.

2. But at this point the identity of the skull with the spinal column ceases, and the very earliest steps in histological differentiation exhibit the fundamental differences between the two. For, in the first place, in no instance save the *Amphioxus*, has the notochord as yet been traced through the whole of the floor of the cranial cavity. In no other embryo has it been yet seen to extend beyond the middle vesicle of the cerebrum, or in other words, beyond the level of the rudiment of the infundibulum and pituitary body.

In the second place, the division into somatomes, in all known vertebrate embryos, stops short at the posterior boundary of the skull, and no trace of such segmentation has yet been observed in the head itself.

3. Apparently as a consequence of these fundamental differences, the further course of the development of the skull is in many respects very different from that of a vertebral column. Chondrification takes place continuously on each side of the notochord, and beyond it, the two trabeculæ cranii, unlike anything in the spinal column, extend along the base of the cranium. No distinct cartilaginous centra, and consequently no intercentra, are ever developed. The occipital arch is developed in a manner remotely similar to that in which the neurapophysial processes are formed; but the walls of the auditory capsules, which lie in front of them, and which give rise to some of the parts, most confidently regarded as neurapophyses by the advocates of the current vertebral theories of the skull, are utterly unlike neurapophyses in their origin.

So, if we seek for hæmal semi-arcs, we find something very like them, arising from the substance of the basis cranii beneath the auditory cartilage; but there is none connected with the occipital cartilage, and none with the rudiment of the alisphenoid. The palatopterygoid cartilage might be regarded as the hæmal semi-arc

of the presphenoidal region, though the grounds for so doing are not very strong; but the premaxillary cartilage is something quite without parallel in the spinal column.

4. The mode of ossification of the skull, and the ultimate arrangement of its distinct bony elements, are at once curiously like, and singularly unlike those presented by the spinal column. The basioccipital is ossified precisely after the manner of a vertebral centrum. Bony matter is deposited around the notochord, and gradually extends through the substance of the cartilaginous rudiment of the part.

The combined basi- and pre-sphenoid in *Pisces* and *Amphibia* is an ossific deposit, which takes place on the under surface of the basal cartilage in front of the basioccipital, and extends thence completely beneath the pituitary interspace as far as the ethmoid. It might be paralleled by the subchordal ossification in the coccyx of the frog, or by the cortical ossification of the atlas in many higher *Vertebrata*, if it really underlay a portion of the notochord; but at the very utmost the notochord only extends into its posterior extremity.

In some of the higher *Vertebrata*, as the snake, the osseous basisphenoid arises in the substance of its cartilaginous rudiment, while the osseous presphenoid underlies its cartilage. In others, both bones appear to arise directly in their cartilaginous forerunners. But nothing can be more irregular than the mode of ossification of the presphenoid, ethmoid and vomer in the vertebrate series, or less like the very constant and regular course of ossification of true vertebral centra.

With respect to the ossification of the lateral and superior constituents of the skull, the development of the exoccipital and supraoccipital does, without doubt, present a very close analogy to that of the separate pieces of the neural arch of some vertebræ in, *e.g.*, a crocodile. The alisphenoids and orbitosphenoids follow in the train of the exoccipitals; but I know not where in the spinal column we are to find a parallel for the double parietals and frontals. But waiving this difficulty, and supposing, for the sake of argument, as was supposed by Oken, that the basisphenoid, alisphenoid and parietals, the presphenoid, orbitosphenoids, and frontals represent the elements of two vertebral centra and neural arches, what is to be made of the petrous and mastoid bones?

The difficulty has been eluded by terming the petrosal a "sense-capsule," the mastoid a "parapophysis." But I apprehend that neither of these explanations can be received for a moment by those who are acquainted with the development of the skull, or with the true homologues of the bones in question in the vertebrate series, or

who think that scientific terms should always possess a well-defined and single meaning.

What, in fact, is the origin of the petrous and mastoid bones? There is much reason for believing (according to Remak's late observations) that the membranous labyrinth is primarily an involution of the sensory or epidermic layer of the blastoderm; but however this may be, it is quite certain that the auditory organ is, primarily, altogether independent of the walls of the skull, and that it may be detached without causing any lesion of them, in young embryos.

It is also quite certain that this membranous labyrinth becomes invested by a coat of cartilage, continuous with the cranial wall; but I do not know that there is evidence, at present, to enable one to say positively, whether this cartilaginous auditory capsule is formed independently around the labyrinth, and then unites with the cranium; or whether it is an outgrowth from the cranial walls, which invests and encloses the labyrinth. If the latter be the case, a consistent vertebral theory of the skull must account for all the bones developed out of the auditory capsule; if the former, it must exclude them all, as parts of an extra-vertebral sensory skeleton.

Now the bones developed in the capsule are, in front, the petrosal; behind, the mastoid; above, the epiotic. The first-named bone is admitted, by the most zealous advocates of the vertebral theory, to be a neurapophysis, in all oviparous *Vertebrata*. Hence they are also bound to admit that, for three centra below and three neural spines bounding the cranial cavity above, there are four pairs of neural arches. More than this, I do not see how it is to be denied that the true mastoid is the morphological equivalent of the petrosal; and in that case there would be five neurapophyses to three central and three neural spines. Furthermore, it is precisely to these two superfluous elements that the only two clear and obvious hæmal arches, the mandibular and hyoid, are attached.

I confess I do not perceive how it is possible, fairly and consistently, to reconcile these facts with any existing theory of the vertebrate composition of the skull, except by drawing *ad libitum* upon the *Deus ex machina* of the speculator,—imaginary "confluences," "connations," "irrelative repetitions," and shiftings of position—by whose skilful application it would not be difficult to devise half a dozen very pretty vertebral theories, all equally true, in the course of a summer's day.

Those who, like myself, are unable to see the propriety and advantage of introducing into science any ideal conception, which is other than the simplest possible generalized expression of observed

facts, and who view with extreme aversion, any attempt to introduce the phraseology and mode of thought of an obsolete and scholastic realism into biology, will, I think, agree with me, not only in the negative conclusion, that the doctrine of the vertebral composition of the skull is not proven, but in the positive belief, that the relation of the skull to the spinal column is quite different from that of one part of the vertebral column to another.

The fallacy involved in the vertebral theory of the skull is like that which, before Von Bär, infested our notions of the relations between fishes and mammals. The mammal was imagined to be a modified fish, whereas, in truth, fish and mammal start from a common point, and each follows its own road thence. So I conceive what the facts teach us is this:—the spinal column and the skull start from the same primitive condition—a common central plate with its laminæ dorsales and ventrales—whence they immediately begin to diverge.

The spinal column in all cases becomes segmented into its somatomes; and, in the great majority of cases, distinct centra and intercentra are developed, enclosing the notochord more or less completely.

The cranium never becomes segmented into somatomes; distinct centra and intercentra, like those of the spinal column, are never developed in it. Much of the basis cranii lies beyond the notochord.

In the process of ossification there is a certain analogy between the spinal column and the cranium, but that analogy becomes weaker and weaker as we proceed towards the anterior end of the skull.

Thus it may be right to say, that there is a primitive identity of structure between the spinal or vertebral column and the skull; but it is no more true that the adult skull is a modified vertebral column, than it would be, to affirm that the vertebral column is a modified skull.[1]

While firmly entertaining this belief, however, I by no means wish to deny the interest and importance of inquiries into the analogies which obtain between the segments, which enter into the composition of the ossified cranium, and the vertebræ of an ossified spinal column. But all such inquiries must start with the recognition of the fundamental truths furnished by the study of development, which, as our knowledge at present stands, appear to me to be summed up in the following propositions:—

1. The notochord of the vertebrate embryo ends in that region of the basis cranii which ultimately lies behind the centre of the basisphenoid bone.

[1] I feel sure that I met with this phrase somewhere, but I cannot recollect its author.

2. The basis cranii is never segmented.

3. The lamina perpendicularis of the ethmoid has the same morphological value as the presphenoid.

4. The petrosal has the same morphological value as the mastoid; if one is not an integral part of the skull, neither is the other.

5. The nasal bones are not neurapophyses.

6. The branchial arches have the same morphological value as the hyoid, and the latter as the mandibular arc.

7. The mandibular arc is primitively attached behind the point of exit from the skull, of the third division of the fifth nerve.

8. The premaxilla is originally totally distinct from the palato-maxillary arcade.

9. The pectoral arch is originally totally distinct from the skull.

Starting on this basis, it might not be difficult to show that the perfectly ossified skull is divisible into a series of segments, whose *analogy* with vertebræ is closer the nearer they lie to the occipital region; but the relation is an analogy and not an affinity, and these cephalic sclerotomes are not vertebræ.

NOTES.

I.—*On the Mastoid in Birds.*

The true mastoid of the bird seems hitherto to have escaped notice.

Hallmann says (*l. c.* p. 33), "In the disarticulated skulls of chickens, I examined the share taken by the different bones in the formation of the labyrinth, by introducing bristles into the semicircular canals, and I found in the proper *petrosum* (into which the facial and acoustic nerves enter, and which contains the cochlea) the anterior crus of the anterior canal (I term the upper one thus for ready comparison with reptiles) and of the external canal; in the supraoccipital, the upper (=posterior) crus of the anterior canal, and the upper end of the posterior canal; and in the exoccipital, the lower crus of the posterior, and the posterior of the external canal. In other words, the distribution of the canals is as in the scaly *Amphibia*. For the rest, in birds as in mammals, and probably in all *Vertebrata*, the membranous semicircular canals are formed connectedly in the cartilage, and the bony parts only gradually invest them. Hence, when the chick's skull is too young, but very little of the posterior canal is to be found in the supraoccipital, which in fact contains somewhat less of the posterior canal than of the anterior, and thereby departs from reptiles and approximates mammals.

"At a certain period also, an interval filled with cartilage, through which the semicircular canals shine, is found in the bird's skull between the supraoccipital, the parietal, the squama temporis, and the exoccipital. I see this clearly in the skull of a young *Dicholophus cristatus* (No. 5605, B.M.). In the skeleton of a young *Colymbus cristatus* (No. 7172, B.M.), I find that this interval is, on the right side, almost filled up by a small bony plate, which has not as yet combined

with the surrounding bones. This appears to me to be a separate *pars mastoidea*, which however combines very early with the exoccipital. In the skull of a young goose (fig. 3) No. 3507, B.M.), this distinct piece (*e* between *s*, *r*, *t* and *l*) is still better shown. Subsequently it is altogether indistinguishable from the exoccipital."

I have endeavoured to show, however, that the true mastoid of the bird is to be sought elsewhere ; and at any rate the bone described by Hallmann has not those relations which he himself considers essential for a mastoid. It appears to me, that the distinct ossification he mentions is the epiotic bone, which has not yet combined with the surrounding parts.

II.—*On the influence of the share taken by the squamosal in the Vertebrate Skull.*

In discussing the homologies of the bones of the skull of the crocodile, Cuvier ('Ossemens Fossiles,' t. ix. p. 163) states that "the squamosal and zygomatic bone becomes more and more excluded from the cranium as we descend in the scale of quadrupeds, so that in Ruminants it is rather stuck upon the skull than enters into the composition of its walls ;" and it is by this argument mainly that the great anatomist justifies his identification of the quadratojugal of the crocodile with the squamosal, or rather with the zygomatic portion of that bone in mammals (*l. c.* p. 171).

Professor Owen ('Principes d'Ostéologie Comparée,' p. 55) adopts Cuvier's argument, and pushes it further, endeavouring to show that the disappearance of the squamosal, and as he supposes of the petrosal, from the interior of the skull in *Reptilia*, is sufficient to account for that retrogression of the alisphenoid behind the exit of the fifth nerve, which is the necessary consequence of his identification of the true petrosal with the alisphenoid.

It seems strange that Cuvier should have advanced so weak an argument as that which I have cited ; for assuredly Ruminants are not very low in the mammalian scale, nor are they those mammals which most nearly approach reptiles or birds. We must seek these among rodents and monotremes, in both of which the squamosal enters largely into the composition of the cranial walls.

This is particularly the case in that especially reptilian mammal the *Echidna*. As to birds, it can still less be said that their squamosal disappears from the interior of the skull. Köstlin says on this point ('Bau des knöchernen Kopfes,' p. 206), "The squamosal contributes a small surface to the ridge, which separates the anterior cranial fossa from the middle one. It is here applied above against the parietal, anteriorly against the anterior, and posteriorly against the posterior sphenoidal ala,[1] and seems in all birds to appear at this point in the cavity of the skull. In the goose its extent is far smaller than in the fowl. The actual size of the ala temporis, however, surpasses that of its inner surface by a great deal. In this respect birds are analogous to the *Cheiroptera*, *Insectivora*, and a few *Marsupialia*, where only a small portion of the squama temporis projects into the cranial cavity. Still more do they resemble the seals, in which this part is entirely enclosed by the parietal and ala temporis, and so is completely separated from the petrosal." Köstlin is in error, however, in assuming that the squamosal is visible in the interior of the skull of all birds, for as we have seen above, such is not the case in the ostrich.

The struthious skull then affords an important test of the value of Professor Owen's argument. If, as he supposes, the disappearance of the squamosal from

[1] Alisphenoid and petrosal, *mihi*.

the interior of the skull causes the alisphenoid to pass behind the exit of the trigeminal, this retrogression ought to have taken place in the ostrich. Nothing of the kind has occurred, however, the trigeminal foramen being a '*trou de conjugaison*' between the alisphenoid and the petrosal. It does not even traverse the middle of the alisphenoid, as in the sheep.

It is unnecessary to discuss the effect of the disappearance of the petrosal, as I have endeavoured to prove that it does not disappear in the lower *Vertebrata.*

III.—*Connexions of the tympanic membrane in Birds.*

According to Köstlin (*l. c.* p. 216), the tympanic membrane of birds is stretched upon a fibrocartilaginous frame, which is ordinarily attached to the squamosal, exoccipital, basisphenoid, and quadratum. In many gallinaceous birds this frame does not come into contact with the quadratum at all. From these circumstances, and from the fact that the quadratum of birds articulates with the lower jaw and the jugal arch, which is never the case with the tympanic of mammals, Köstlin concludes, with great justice, that the quadratum is not the homologue of the mammalian tympanic.

IV.—*On the modifications of the palatosuspensorial arch in Fishes.*

I have very briefly stated my views on this subject in the Quarterly Journal of Microscopical Science for October 1858, hoping at that time to enter more largely upon the subject in this place. But the present Lecture and its notes already occupy so much space, that I must reserve a full statement of what I have to say respecting the palatosuspensorial apparatus of fishes for a future occasion.

V.—*On the development of the Cranium.*

In confirmation of the views which I have adopted, as to the primary uniformity of plan of all vertebrate crania, I subjoin an abstract of Rathke's most valuable account of the development of the skull in *Coluber natrix*,[1] which contains much incidental information relating to the development of the skull in *Vertebrata* in general. Vogt's observations on *Coregonus* and *Alytes*, and my own on *Gasterosteus*, *Rana* and *Triton*, are in entire accordance with those of Rathke, so far as the primitive structure of the basis cranii is concerned.

The differences between the basis of the skull and the vertebral column in the earliest embryonic conditions are,—

1. That round that part of the chorda which belongs to the head, more of the blastema, that is to be applied, in the spinal column, to the formation of the vertebræ and their different ligaments, is aggregated than around the rest of its extent, and—

2. That this mass grows out beyond the chorda to form the cranial trabeculæ.

The lateral trabeculæ at their first appearance formed two narrow and not very thick bands, which consisted of the same gelatinous substance as that which constituted the whole investment of the chorda, and were not sharply defined from the substance which lay between them and at their sides, but seemed only to be two thickened and somewhat more solid, or denser, parts of that half of the basis of the cranium which lies under the anterior cerebral vesicle.

Posteriorly, at their origin, they were separated by only a small interval, equivalent to the breadth of the median trabecula, and thence swept in an arch to

[1] Entwickelungsgeschichte der Natter,' 1839

about the middle of their length, separating as they passed forwards; afterwards they converged, so that, at their extremities, they were separated by a very small space, or even came into contact. Altogether they formed, as it were, two horns, into which the investing mass of the chorda was continued forwards. The elongated space between them, moderately wide in the middle, was occupied by a layer of softer formative substance, which was very thin posteriorly, but somewhat thicker anteriorly. Upon this layer rested the infundibulum; and in front of it, partly on this layer, partly on the trabeculæ, that division of the brain whence the optic nerves proceed, and further forwards the hemispheres of the cerebrum. Anteriorly, both trabeculæ reached as far as the anterior end of the head, and here bent slightly upwards, so that they projected a little into the frontal wall of the head, their ends lying in front of the cerebrum. Almost at the end of each horn, however, I saw a small process, its immediate prolongation, pass outwards and form, as it were, the nucleus for a small lateral projection of the nasal process of the frontal wall.

The middle trabecula grows, with the brain, further and further into the cranial cavity, and as the dura mater begins to be now distinguishable, it becomes more readily obvious than before, that the middle trabecula raises up a transverse fold of it, which traverses the cranial cavity transversely.[1] The fold itself passes laterally into the cranial wall; it is highest in the middle, where it encloses the median trabecula, and becomes lower externally, where it forms, as it were, a short ala proceeding from the trabecula. With increasing elongation, the trabecula becomes broader and broader towards its free end, and, for a short time, its thickness increases. After this, however, it gradually becomes thinner, without any change in its tissue, till, at the end of the second period, it is only a thin lamella, and after a short time (in the third period) entirely disappears.

In mammals, birds, and lizards, that is, in those animals in general, in which the middle cerebral vesicle is very strongly bent up and forms a protuberance, while the base of the brain exhibits a deep fold between the infundibulum and the posterior cerebral vesicle, a similar part to this median trabecula of the skull is found.

In these animals, also, at a certain very early period of embryonic life, it elevates a fold of the dura mater which passes from one future petrous bone to the other, and after a certain time projects strongly into the cranial cavity. Somewhat later, however, it diminishes in height and thickness, as I have especially observed in embryos of the pig and fowl, until at last it disappears entirely in these higher animals also, the two layers of the fold which it had raised up coming into contact. When this has happened, the fold diminishes in height and eventually vanishes, almost completely.

The two lateral trabeculæ, which in the snake help to form the anterior half of the basis of the skull, attain a greater solidity in the second period, acquire a greater distinctness from the surrounding parts, and assume a more determinate form, becoming, in fact, filiform, so that the further forward, the thinner they appear. They increase only very little in thickness, but far more in length, during the growth of the head. Altogether anteriorly, they coalesce with one another, forming a part which lies between the two olfactory organs and constitutes a septum. As soon as these organs increase markedly in size, this part is moderately elongated and thickened, without however becoming so dense as the hinder, longer part of the trabeculæ. The prolongations into the lateral projections

[1] What Rathke terms the 'middle trabecula,' appears to be only very indistinctly developed in *Fishes* and *Amphibia*.

of the nasal processes, which now proceed from the coalesced part in question, also become but little denser in texture for the present, though they elongate considerably.

The lateral parts and the upper wall of the cranium, with the exception of the auditory capsules or of the subsequent bony labyrinth, remain merely membranous up to the end of the second period, consisting in fact only of the cutaneous covering, the dura mater, and a little interposed blastema, which is hardly perceptible in the upper part, but increases in the lateral walls, towards the base of the skull.

The chorda vertebralis reaches, in very young embryos of the snake, to between the auditory capsules, and further than this point it can be traced neither in the snake nor in other *Vertebrata*, at any period of life, as manifold investigations, conducted with especial reference to this point, have convinced me.

At the beginning of the third period, the basal plate chondrifies, at first leaving the space beneath the middle of the cerebellum membranous ; but this also eventually chondrifies, and is distinguished from the rest of the skull only by its thinness.

Lateral processes grow out from the basal cartilage just in front of the occipital foramen, and eventually almost meet above. They are the exoccipitals.

The two lateral trabeculæ, parts which I have also seen in frogs, lizards, birds, and mammals, chondrify at the beginning of the third period. At first, they pass, separate from one another throughout their whole length, as far as the frontal wall, on entering which they come into contact ; are more separate posteriorly than anteriorly, and present, in their mutual position and form, some similarity with the sides of a lyre. But as the eyes increase, become rounder, and project, opposite the middle of the trabeculæ, downwards towards the oral cavity, the latter are more and more pressed together, so that even in the third period they come to be almost parallel for the greater part of their length. Anteriorly, however, where they were already, at an earlier period, nearest to one another, they are also pressed together by the olfactory organs (which have developed at their sides to a considerable size), to such a degree, that they come into contact for a great distance and then completely coalesce ; they are now most remote posteriorly, where the pituitary body has passed between them,[1] so that they seem still to embrace it. Anteriorly, between the most anterior regions of the two nasal cavities, they diverge from their coalesced part as two very short, thin, processes or cornua, directed upwards, and simply bent outwards.

" It has been seen above that the median trabecula does not chondrify, but eventually disappears ; in its place, a truly cartilaginous short thick band grows into the fold of dura mater from the cartilaginous basal plate.

" Where the pituitary gland lies, there remains between the lateral trabeculæ of the skull a considerable gap, which is only closed by the mucous membrane of the mouth and the dura mater. But there arises in front of this gap, between the two trabeculæ, as far as the point where they have already coalesced, a very narrow, moderately thick, and anteriorly pointed streak of blastema, which, shortly before the end of the third period, acquires a cartilaginous character, and subsequently becomes the body of the presphenoid.[2]

[1] The pituitary body, however, as Rathke now admits, does not pass between the trabeculæ, and is developed in quite a different manner from that supposed in the memoir on *Coluber*.

[2] Compare with these statements, the figures and descriptions given above of the embryonic cranium in *Gasterosteus* and *Rana*.

"Altogether anteriorly, however, where the two trabeculæ have coalesced, there grows out of this part, from the two cornua in which it ends, a pair of very delicate cartilaginous plates. At the end of the third period both plates acquire a not inconsiderable size, take the form of two irregularly formed triangles, and are moderately convex above, concave below, so as to be on the whole, shell-shaped. The nasal bones are developed upon these, while below them are the nasal cavities, and the nasal glands with their bony capsules.

"The alæ or lateral parts of the two sphenoids do not grow like the lateral parts of the occipital bone out of the basis cranii, whose foundation is formed by the cephalic part of the chorda, but are formed separately from it, although close to it, in the, until then, membranous part of the walls of the cranium.

"The alæ of the presphenoid (orbitosphenoids), which are observable not very long before the termination of the third period, appear as two truly cartilaginous (though they never redden), irregular, oblong, plates of moderate thickness, lie in front of the optic foramina, at the sides of the lateral trabeculæ of the skull, ascend from them upwards and outwards, and are somewhat convex on the side turned to the brain, somewhat concave on the other. The alæ magnæ (alisphenoids) are perceptible a little earlier than these. They are formed between the eye and the ear, and also originally consist of a colourless cartilaginous substance; they appear at the end of the third period as irregular four-sided plates, lie at both sides of the anterior half of the investing plate of the chorda, ascend less abruptly than the alæ orbitales, and are convex externally, internally concave.

"The upper posterior angle of each elongates, very early, into a process, which grows for a certain distance backwards, along the upper edge of the auditory capsule, and applies itself closely thereto.

"The auditory capsules, or the future petrous bones,[1] chondrify, as it would appear, the earliest of all parts of the skull: the fenestra ovalis arises in them by resorption.

"The *ossification* of the snake's skull commences in the basioccipital, or at any rate, this is one of the first parts to ossify. At a little distance from the occipital foramen, there arises a very small semilunar bony plate, whose concave edge or excavation is directed forwards; thereupon the bony substance shoots from this edge further and further forwards, until at length the bony plate has the form of the ace of hearts. Its base borders the fontanelle in the base of the skull, which lies under the anterior half of the third cerebral vesicle, while its point is contiguous to the occipital foramen; for the most part it is very thin, and only its axis (and next to this its whole posterior margin) is distinguished by a greater thickness. The cephalic part of the chorda can be recognized in the axis of this bony plate up to the following period. It passes from the posterior to the anterior end of the bony plate, where it is lost, and is so invested by the bony substance of the plate, that a smaller portion of the latter lies on the upper side of the chorda, a larger portion beneath it. On this account it forms, on the upper side of the plate, a longitudinal ridge, which subsequently becomes imperceptible by the aggregation of matter at the sides. On one occasion, however, I saw, in an embryo which was almost at term, a similarly formed and sized bony cone, which, through almost its entire length, appeared merely to lie *on* the body of the basioccipital, since it had only coalesced with it below."

The nucleus and sheath of the cephalic part of the chorda become gradually broken up and the last trace of them eradicated, as the ossification of the basi-

[1] It will be found from Rathke's statements, further on, that the future petrous bone only represents a portion of each auditory capsule.

occipital proceeds, like the nucleus and sheath of the rest of the chorda wherever a vertebral body is developed.[1]

The articular condyle is not yet formed. The exoccipitals ossify through their whole length and breadth.

The body of the basisphenoid is formed between the above-mentioned posterior fontanelle of the basis cranii and the pituitary space, 'therefore far from the cephalic part of the chorda.' It ossifies by two lateral centres, each of which forms a ring round the carotid canal. The alisphenoids ossify in their whole length and breadth; the orbitosphenoid only slightly, and the presphenoid not at all. The premaxillary bone arises as an azygos triangular cartilage between the cornua of the anterior ethmovomerine plate. It ossifies from a single centre.

"The auditory capsule, or the future petrosal bone, may, even at the end of this period, be readily separated from the other part of the cranial wall, and still consists for the most part of cartilage. On the other hand, the triangular form, which it had before, is not inconsiderably altered, since it greatly elongates forwards, and thus, as it were, thrusts its anterior angle further and further forwards, and becomes more unequal-sided. At the lower edge, or the longer side of it, about opposite to the upper angle, at the beginning of this (third) period, or indeed somewhat earlier, a diverticulum of the auditory capsule begins to be formed (the rudimentary cochlea), and developes into a moderately long, blunt, and hollow appendage, whose end is directed downwards, inwards and backwards, and also consists of cartilage. Close above, and somewhat behind this appendage, however, there appears, at about the same time, a small rounded depression, in which the upper end of the auditory ossicle eventually rests; and somewhat later, an opening appears in this depression which corresponds with the fenestra rotunda of man. Very much later, namely, towards the end of this period, the auditory capsule begins to ossify. Ossification commences in a thin and moderately long, hook-like process, which is sent forwards and inwards from the lower hollow diverticulum of the cartilage, and unites with the basisphenoid. From this point it passes upwards and backwards, and, for the present, extends so far that, at the end of this period, besides that process, the diverticulum in question and about the anterior third of the auditory capsule itself, are ossified. Later than at the point indicated, an ossific centre appears at the posterior edge of the auditory capsule, where it abuts against the supra- and ex-occipitals, but extends from hence by no means so far forward as to meet that from the other point. The middle, larger part of the auditory capsule, therefore, for the present, remains cartilaginous.

"In the beginning of the fourth period, a third ossific centre arises in the upper angle of the capsule, whereupon all three grow towards one another. But the mode of enlargement and coalescence of these bony nuclei is very remarkable. They do not unite with one another in such a manner as to form a continuous bony capsule for the membranous part of the labyrinth, but are permanently separated by cartilagino-membranous and very narrow symphyses. On the other hand, one coalesces, in the most intimate manner, with that edge of the supraoccipital which is nearest to it, so that even in the more advanced embryos, this bone and it form a moderately long oblong plate, each end of which constitutes a small, tolerably deep, and irregularly-formed shell, containing a part of the anterior or upper semicircular canal. The second bony centre becomes an-

[1] In the stickleback it has appeared to me that the wall of the anterior conical termination of the notochord in the basis cranii becomes ossified, or at any rate, invested by an inseparable sheath of bony matter, just in the same way as the 'uro style' is developed in the tail.

chylosed with the anterior edge of the lateral part of the occipital bone, and also forms a small, irregularly-shaped, but longish scale, which contains the deeper or lower part of the posterior crus of that semicircular canal, and besides this, the lower sac, or representative of the cochlea of the auditory labyrinth. The remaining bony mass of the auditory cartilage, however, includes the greater part of the membranous portion of the labyrinth, and is the largest. The same phenomenon, viz. that the petrosal bone breaks up, as it were, into three pieces, of which two coalesce with the occipital bone, occurs also, according to my observations, in *Lacerta agilis*, and probably takes place in like manner, if we may conclude from the later condition of the petrous bone to the earlier, in *Crocodilia* and *Chelonia*. A squama temporis and a mastoid are, as I judge, never formed in *Ophidia*."

Yet what is the osseous mass which eventually coalesces with the exoccipital but the mastoid? I have indicated above what I believe to be the true ophidian squamosal.

VI.—*On the development of the Ossified Vertebral Column.*

The concise statement of the general nature of this process which I have given above, is based, partly on the observations of Vogt, Rathke, and Remak, and partly on my own. As great misunderstanding seems to me to have prevailed on this head, I have put together in the present note, all the most important evidence I have been able to collect on this highly interesting subject, accompanying it with a running commentary. I have done this the more willingly, as the accounts of the mode of development of vertebræ in general, in our own language, which I have met with, are strangely meagre.

Development of the Spinal Column in Fishes.

1. *Blennius viviparus* (Rathke, 'Bildungs- und Entwickelungsgeschichte des *Blennius viviparus*.' 1833).

The surface of the notochord hardens, and acquires a fibro-membranous consistence, while its inner substance becomes glassy and transparent, so that the notochord is separated into sheath and contents, as in the lamprey. A segmentation next takes place in the sheath. "At successive intervals it increases, more and more, in density and solidity, acquires in places almost the constitution of cartilage, and there thus arise a great number of successive, very fine, narrow rings, which are connected by much narrower, far less solid, but also far less transparent and more whitish-coloured parts, like sutures."

When this segmentation has commenced, "a number of cartilaginous, very short, thin and rod-like processes, which run in pairs from each member of the vertebral column, where its upper side passes into the two outer ones, appear, pass upwards in the walls surrounding the spinal marrow, and enclose its lower cords. At first, therefore, each pair of processes are separated by a considerable interval throughout their entire length. Subsequently their upper ends approximate (increasing in length, and at the same time accommodating themselves to the curve of the spinal marrow, and bending round it) more and more closely, till they, at last, meet above the spinal marrow, and soon after this has happened, coalesce into an arch.

"Contemporaneously with these processes, and in the same way, there arise from the vertebral column (though only from its hinder half, or that which constitutes the foundation of the tail) a number of other processes similar in form and structure, which spring from the junction of the under with the lateral faces of the

column. These take the opposite direction to the preceding, tend to enclose the great caudal vessels, and unite in pairs into arches, which lie in a series and correspond with the vertebral segments."

From the segments of that part of the vertebral column which lies between the tail and the head, there grow out, in corresponding places to those in which the crura of the inferior arches take their origin from the vertebral segments of the tail, and in the same manner and at the same time, many cartilaginous processes, which attain, however, only a very slight length, and also take a transverse direction. They might be regarded as lateral pieces of the transverse processes of the higher animals; but it is more probable that they correspond with the ribs of other *Vertebrata*.

"All these processes are connected with the sheath, but not with the core of the notochord."

As development advances, the ring-like segments increase in breadth, length and thickness; at the same time they become somewhat cartilaginous, and then ossify. Each widens somewhat more at its ends than in the middle, and so appears a little contracted in the centre. It is only after birth that such an internal thickening takes places as to interrupt the cavity of the vertebral centrum.

The sheath of the notochord is originally of one texture throughout, but the smaller portions, which lie between the vertebral centra, assume a fibrous texture, contemporaneously with the appearance of the latter. The included substance of the notochord loses its peculiar dense and elastic character, becomes first gelatinous, then grumous, and finally resembles a thick serum.

The crura of the upper and lower vertebral arches (in the tail) unite in pairs, and their points of union grow out into spinous processes.

The ossification of the processes which arise from the vertebræ commences at the point of junction of the process with the centrum. "A small bony point arises, which appears to belong to both centrum and process, and from whence ossification extends into both. In each vertebral centrum, therefore, as well of the tail as of the trunk, ossification proceeds from different and distant points."

2. *Cyprinus blicca* (Von Bär, 'Untersuchungen über die Entw. d. Fische.' 1835).

"At the end of the first day the notochord is covered by something which surrounds it like thin plates; these are the developing bodies of vertebræ. It is clearly observable that these bodies of vertebræ are not undivided rings surrounding the notochord, but that they consist of many pieces united by sutures. This condition also is persistent in the sturgeons. The body of the vertebræ, therefore, is formed of the coalescence of many pieces, and a lateral suture seems to indicate that these processes are elongations of the previously observed upper and under vertebral arches."

Von Bär imagines that the unconstricted part of the notochord gives rise to the intervertebral ligaments.

From these observations of Rathke and Von Bär, it would appear as if the annular ossifications which surround the notochord arose by the coalescence of ossific centres, primarily developed at the junction of the apophyses with the centra. My own observations on *Gasterosteus*, however, show, like those of Vogt on *Coregonus*, that the centra ossify from distinct rings deposited immediately round the notochord; and I am very strongly inclined to believe that the corresponding primary annular diaphyses of the vertebræ in *Cyprinus* and *Blennius* have been overlooked.

3. *Coregonus palea* (Vogt, 'Embryologie des Saumones,' 1842, p. 104, *et seq.*).—

"But it is necessary to distinguish carefully between what we call vertebræ in the adult fish, that is to say, those osseous or cartilaginous pieces intended for the support of the whole body, and more particularly of the spinal cord, and such vertebral divisions as we find in embryos. These last are the general fact, the expression of a constant law according to which all the *Vertebrata* are developed. The vertebræ of adult fishes, on the other hand, are solid rings, whose presence depends on the type peculiar to each species; consequently their form, and the substance of which they are composed, vary in almost every species.

"The vertebral divisions[1] appear very early in the *Coregonus*—almost at the same time as the notochord; and when the dorsal groove begins to close, they are fine lines, caused, as it would appear, by a greater accumulation of embryonic cells, which, like transverse septa, traverse the entire mass as far as the notochord. These divisions extend forwards, as far as the neighbourhood of the auditory vesicles, but there never exists the smallest trace of them in the head itself. At first they are visible only in the middle of the body; by degrees they move forwards, as far as close to the ear, and backwards, towards the tail, as far as it is formed; but they invade its extremity only when it has attained its full length relatively to the body. At first these lines are all straight and perpendicular to the axis of the chorda; but by degrees, and in proportion as development advances, they become oblique and bend, forming an angle whose apex is directed forwards, and corresponds exactly to the median line of the notochord."

They eventually become the intermuscular septa. Vogt goes on to say,—"The typical structure of the *Vertebrata*, then, consists solely in these rings of separation, which are formed around a notochord, and nowise in the development of a distinct head, or of other solid pieces of the skeleton, such as osseous or cartilaginous vertebræ," illustrating his case by the *Amphioxus*.

Each osseous vertebra corresponds to two vertebral segments, namely, to the half of that which precedes, and to the half of that which follows a metasomatome; for it is where the latter reaches the notochord, that the centra and arches take their origin. The centra arise as a double ring of cartilage, internal and external to the sheath of the notochord. The intervertebral spaces always correspond with the middle of the interval between two intermuscular septa, each of which is consequently inserted into the middle of a centrum, while the superior and inferior arches are developed in their plane. They are ossified only long after the centra, which arise as bony rings around the notochord. The intervertebral ligaments are formed from the sheath of the notochord.

4. Prof. Owen ('Principes d'Ostéologie Comparée,' 1855, p. 184) affirms that "In osseous fishes the centrum is ordinarily ossified from six points, of which four begin in the bases of the two neurapophyses and of the two parapophyses, but the terminal concave plates of the centrum are ossified separately."

It is not stated on what fish the observations on which this latter assertion is based were made. Prof. Williamson has already shown ('On the Development of the Scales and Bones of Fishes,' Phil. Trans. 1851) that it is inconsistent with the structure of the adult vertebra; it is not supported by any of those writers who have directly observed the development of the vertebræ of Teleostean fishes, and it is negatived by the observations of Vogt just cited and by my own.

Development of the Spinal Column of Batrachia.

1. *Anura* (Dugès, 'Recherches sur les Batraciens,' 1835).—In the first period the notochord appears to be divided transversely into "rondelles" or vertebræ, but

[1] Metasomatomes, their interspaces being the somatomes.

these are not real divisions; they are appearances produced by the intersections of the muscles which surround the notochord, and of the transverse vascular branches which accompany each pair of nerves when it leaves the medulla. [Dugès thus describes the somatomes.]

In the second period cartilaginous processes, adherent to the notochord, appear in pairs and enclose the medulla. There are as many of these processes as vertebræ will in future exist, and two crests even make their appearance, to form the walls of the coccygeal canal. The apophyses are at first little tubercles; they then bifurcate; one branch becomes the transverse process, the other the neurapophysis with its zygapophyses. In *B. fuscus*, *A. obstetricans*, *punctatus*, and *Hyla*, where these vertebræ ossify, "two clouds" of ossific matter make their appearance in each vertebra, "as distant from one another as they are from the lateral masses or apophyses," and eventually unite above the notochord so as to form a quadrate ossific centre. This quadrate mass enlarges, but remains concave, not only above, but also in front and behind, and especially below, where it forms a semi-canal or groove, in which the notochord is lodged. The groove is gradually filled up, the notochord undergoing a contemporaneous atrophy, and becoming eventually reduced to a mere ligament. The intervertebral masses are formed altogether independently of the notochord.

In *Rana*, on the other hand, the primitive centre of ossification of the body of the vertebra is a ring completely enclosing the chorda; in other respects the development of the spinal column resembles that just described.

2. Müller ('Vergleichende Anat. d. Myxinoiden,' 1835) remarks, "that the formation of the primitive elements of the skull (which are different from the secondary osseous ones) takes place in the higher animals, constantly in the same way, is much to be doubted, since variations of the fundamental plan obtain in the vertebral column. In many *Batrachia*, as *Cultripes provincialis*, and *Rana paradoxa*, the bodies of the vertebræ arise only out of the upper primitive vertebral elements. I found, indeed, in the larva of *Rana paradoxa*, on the under part of the circumference of the chorda dorsalis, a cartilaginous band which was especially well developed posteriorly, in front of the ossification of the coccygeal spine, and was continued, thinner, along the under surface of the chorda, for half the length of the future vertebral column. This cartilaginous band had no fellow, but on the contrary, was thickest in the middle. In the caudal part of the chorda it diminished until it gradually disappeared, so that the inferior arches surrounding the caudal vessels were merely fibrous productions of the external sheath of the chorda. But this inferior cartilaginous band on the chorda of the larva of *Rana paradoxa* disappears in the greater part of the spinal column, and merely a part of it ossifies to become the basilar part of the coccyx, which Dugès was acquainted with, as well as with the two vertebræ of the coccyx above the chorda; the basilar bone is not a body of a vertebra, but coalesces subsequently with the inferior circumference of the coccygeal vertebræ. In these frogs, the coccyx is the only part which arises from both upper and lower vertebral elements; all the other vertebræ arise in *Cultripes* and *Rana*, merely from the upper primitive vertebral elements, which in the course of ossification become divided into arches and central portions. It is only the ossifications of the coccyx which, in these frogs, completely enclose the chorda, since that part is eventually composed of two pairs of vertebræ, and a long basilar piece, whose sutures are retained even in the adult *R. paradoxa*" (p. 130).

3. *Alytes*.—With respect to the development of the vertebræ in *Alytes obstetricans*, Vogt ('Entwickelungsgeschichte der Geburtshelferkröte,' 1842) states that cartilaginous rings appear in the sheath of the chorda, as rudiments of the

centra. Contemporaneously with these the cartilaginous neural arches are developed in the wall of the canal of the medulla ; nothing is said as to the mode of ossification.

4. In both *Rana temporaria* and *Triton*, I find that the diaphysis of the vertebra arises as a saddle-like patch, upon, and in immediate contact with, the dorsal surface of the notochord ; the layer of osseous matter is at first exceedingly thin, and gradually extends round the notochord until in most of the frog's vertebræ, and in all of those of the *Triton*, it forms a complete ring. The osseous deposit in the arches is quite distinct, and has, in the frog, the form of a thin bony sheath investing their cartilaginous basis. The diaphysis of the sacral vertebra remains open below long after the others, and after its neural arch is completely ossified.

5. The development of the coccyx of the anourous *Batrachia* has been well described by Dugès (*l. c.* p. 108). The two neural arches originally formed in this region ossify and unite above the spinal cord, and at the same time two osseous centra, which very soon coalesce with them, are formed. These centra are incomplete arcs, open below, where they embrace the notochord. A long cartilaginous plate, however, arises on the ventral surface of the notochord, extending backwards far beyond the level of these posterior coccygeal vertebræ. It ossifies, and eventually becomes anchylosed with the bodies of the coccygeal vertebræ to form the coccyx. Such is the substance of Dugès' views, which, as has been seen, have been confirmed in all essential points by Müller.

Prof. Owen, however, gives a very different account of the matter.

"The vertebræ of the tail of the larvæ of the *Anura* are seen distinctly only in the aponeurotic stage. When chondrification occurs, the operation of absorption and coalescence takes place, and two long neurapophyses only are established on each side ; the ossification of these plates extends into the fibrillar sheath of the rest of the coccygeal notochord, and when the perishable parts of the tail of the larva have been absorbed, and the fore- and hind-legs are developed, they constitute by their connation the elongated, osseous coccygeal style, often hollow, of the anourous *Batrachia*." ('Principes d'Ostéologie,' 1855, p. 186.)

Prof. Owen does not state on what anourous batrachian his observations were made, nor does he notice the wide discrepancy between his views and those of Dugès. I have carefully studied the development of the coccyx in the common frog, and my observations are in entire agreement with those of Dugès. Nothing can be more clear than the primitive entire independence of the inferior cartilaginous plate, which by its ossification constitutes the major part of the coccygeal style, from the two neurapophyses and the rudimentary diaphyses which correspond with them.

Development of the Spinal Column of Reptilia.

1. *Ophidia* (Rathke, 'Entw. der Natter,' 1839).—"Quadrate plates of a more solid substance than the rest of the blastema appear on each side of the notochord, in the middle of the body, where they are at first largest, diminishing in size backwards and forwards. At first they extend neither into the dorsal nor into the ventral plates of the embryo.

"These plates increase in length, and those of each pair grow towards one another above and below. Each plate grows out into two branches above and below. The inner branches lie in close contact with the notochord, and coalesce with those of the opposite side, so as to form rings which eventually become the bodies of the vertebræ. The upper outer branch extends into the wall of the

neural canal, and, eventually uniting with its fellow, forms the neural arch. The lower outer branch extends into the ventral wall and becomes the rib."

The ring grows both externally and internally, so as to constrict the notochord (which softens and acquires a grumous consistence), and then becomes converted into bone, so that the notochord is surrounded by a series of bony rings. The notochord takes no part in the formation of the articular intervertebral surface, which is an apophysis and not an epiphysis ; the neural arches ossify much later than the centrum, from a single point in the middle of each. The inferior processes are outgrowths of the substance of the vertebra, and in the caudal region are, from the first, double.

" On each side of the body of the vertebra, where the ribs and the vertebral arches radiate from it, the condensed blastema of which it originally consists, grows out slowly, but considerably, and becomes developed (gradually undergoing chondrification) into a plate, whose largest surfaces are vertical, which increases more in length than in breadth and thickness, and which gradually drives the rib and vertebral arch further away from the axis of the vertebral column. At the end of this period it is almost as thick as the length of the vertebræ ; it then appears, when viewed from in front or behind, as a short irregular oblong, one of whose angles psases into the body of the vertebra, and one of whose shorter sides is turned outwards and upwards. From this side passes one crus of the vertebral arch, while from the side which is turned outwards and downwards, at least in most of the vertebræ, a rib is developed, so that these processes are connected with the originally existing part of the body of the vertebra, only mediately, by the plate in question.

" The crura of the vertebral arch ossify from their middle towards both ends, the process commencing very soon after the ossification of the centra ; but after ossification has begun in them, these originally filiform parts widen into broad oblong plates, which, in the greater part of the body, come into contact only towards the end of the period, and in the tail and hindermost part of the body, only in the following period.

" The ribs ossify far later, and also from the middle towards the end. Before, however, an ossific centre is developed in them, the cartilage, of which the rib now for the most part consists, becomes articulated with the rest of the vertebra. The plate, lastly,[1] which forms the union between a rib, a vertebral arch and a vertebral body, and subsequently forms a part of the body of the vertebra, ossifies only in the following period.

" The relation of the ribs to the bodies of the vertebræ, therefore, is originally just the same as that of the crura of the vertebral arches to them : just as one of these crura, does each rib arise as an outward growth of that vertebral body which is the first formed of all these parts ; whilst, however, the crura of the vertebral arches are directed upwards in order to enclose the spinal cord, the ribs grow downwards to enclose the viscera of organic life, and in this way their greater length in the snake, and a multitude of other *Vertebrata*, is explicable.

" The transverse processes of the caudal vertebræ exhibit the same relations to the bodies of the vertebræ, as the ribs in the dorsal region. They arise in the same places as these ; become, in like manner, removed, together with the crura of the arches, by lateral outgrowths of the body from its axis ; and, before the ribs are articulated, they pass quite imperceptibly into the processes in question. The transition is the more remarkable, as in the snake the hindermost rib is split, in

[1] Paraphysial cartilage.

just the same manner as the transverse processes of the three or four succeeding caudal vertebræ.

"If we consider, in the first place, the relation of the parts in the adult snake, we find that the penultimate rib, near its upper or inner end, gives off from its upper side, a small process directed upwards and outwards ; however, in the last rib this process is about a quarter as long as the remaining part of the rib, which lies external to and below it, so that the whole bone has the form of a two-pronged hay-fork, not yet fastened to a handle, and one of whose prongs is for the most part broken off. The same fundamental form is possessed by the transverse process of the first caudal vertebra ; and the difference between it, and the rib which lies immediately before it, lies principally in this, that it is not, like the rib, articulated with its vertebra, that its upper half or prong is almost equal in length to the lower, and that, regarded as a whole, it is not half so long as the hindermost rib. The transverse processes of the succeeding caudal vertebræ have quite the same form as their predecessors, but gradually diminish in length backwards. As to the development of the ribs and transverse processes in question, they, like almost all the other ribs, are originally sent out as quite simple rays from the bodies of their vertebræ ; very soon, however, there arises on the upper side and neck of the ray where it passes out from the vertebral body, an outgrowth which elongates more or less, also assumes a ray-like form, and has its free end directed outwards. Thus a fork is produced, whose one prong is more or less thicker than the other."

Rathke suggests that the accessory ribs of many fish are probably developed in this way, the upper prong becoming articulated with the lower.

"The two or three anterior subvertebral processes in the tail are, and remain, quite simple, like the similar processes of the cervical and many dorsal vertebræ. The two halves of the others, which arose as separate lateral processes, remain permanently distinct.

"All the newly commencing inferior processes arise as paired outgrowths of the bodies of the vertebræ."

"The ribs are not less outgrowths (*ausstrahlungen*) of the bodies of the vertebræ than the crura of the arches, as I can say from my investigations on fishes, snakes, lizards, birds, and mammals ; even when the bodies of the vertebræ are completely chondrified, the ribs form a connected whole with them, but subsequently they become articulated, and are thereby essentially distinguished from the crura of the vertebral arches. In some animals the articulation takes place and remains close to the bodies ; in others it takes place also close to the bodies, yet, afterwards, a process grows out between the rib and the body, by which the rib is more or less thrust out ; this is the transverse process ; where it occurs, the rib is, in all cases, at first united only with it ; sometimes, however, a process grows out from the rib (the so-called head with its neck), by which it becomes immediately attached to the body of the vertebra itself, so that it is doubly united with the body. In many cases the rib may also become articulated at some distance from the body, and thus break up into rib and transverse process."

"As respects the ribs of the higher *Vertebrata*, together with their transverse processes, the development of the snake teaches us, that although they are subsequently seen to be in close connexion with the crura of the vertebral arches, they grow out, not from the base of these arches, but far from them, out of the bodies of the vertebræ themselves ; where they have arisen, however, each lateral half of the body of the vertebra increases in thickness, in such a manner that it acquires an ala, which drives the crus of the vertebral arch and the rib further

and further from the axis, until at length it appears as a common trunk for both, and therefore may easily deceive one into supposing, that the rib is given off from the base of the crus of the arch, and is a process from it."

2. "*Lacertilia* (Rathke, 'Ueber die Entwick. d. Schildkröten,' 1848, pp. 65–67).—In the lizards (as in the snakes), the osseous centra of the vertebræ appear as rings, which do not so closely embrace the notochord (as they do in fishes and Batrachia), being separated from it by a layer of cartilage.

3. *Chelonia* (Rathke, 'Schildkröten,' p. 65–67).—In the *Chelonia* two bony rings arise, the one on the outer surface of the cartilaginous basis of the centrum, the other close to the notochord; the rings thicken and eventually coalesce; the ossification of the arches takes place quite independently of that of the centrum. The notochord takes no essential part in the formation of the articulations between the vertebræ, but runs like a thread through them.

Development of the Spinal Column of Birds.

In the Chick (Remak, 'Untersuchungen über die Entw. die Wirbelthiere,' 1855).—The upper and middle (sensory and motor) layers of the germ coalesce to form the axial plate (primitive streak); the lateral halves of this plate thicken and leave between them a groove, the primitive groove, immediately below the groove, and parallel with it, the notochord appears in the axis of the motor layer. The sensory layer of the axial plate is now the medullary plate; from it the nervous centre is developed; the motor layer is termed by Remak the 'Urwirbel-platte,'—the primitive vertebral plate.

The primitive vertebræ (Urwirbel, somatomes) first appear in the dorsal part of the embryo, as opaque portions of the substance of the primitive vertebral plates, which extend from the sides of the chorda into the lateral plate, or that thickened part of the motor layer with which the primitive vertebral plates are immediately continuous. These primitive vertebræ are the result of a sort of segmentation of the motor layer; they acquire a cubical form, and are separated by clear, narrow interspaces (metasomatomes).

At the beginning of the third day the ventral surface of each primitive vertebra has an almost square shape with rounded angles; the transverse section is no longer square but three-sided, the upper and outer faces having merged into one convex face; the surface turned towards the medullary canal is four-sided and a little concave.

The inferior internal edge of the primitive vertebra grows out towards the notochord, and having reached its outer side, it divides into two lamellar processes, which, coalescing with those of the other side, surround the notochord and constitute the blastema of the vertebral column.

The dorsal layer of the primitive vertebra becomes converted into muscle, and forms a segment of the dorsal muscles; the anterior portion of its substance, beneath this, becomes the spinal ganglion; the posterior, the rudiment of the neural arch and rib. The latter extends backwards beyond the boundary of its primitive vertebra into the region of the next, so that it appears to be divided by the clear line of separation into a larger anterior and smaller posterior portion.

The axial portion of the vertebral column does not become segmented in correspondence with the divisions between the primitive vertebræ, but midway between them, so that the lines of separation between the primitive vertebræ correspond with the centres of the permanent vertebræ, each of which may thus be said to be formed by the coalescence of the posterior half of the axis of one primitive vertebra with the anterior half of the next following.

Rathke, 'Schildkröten,' p. 66.—In birds, the centra commence as bony rings which closely encircle the chorda, and lie internal to the general cartilaginous mass of the vertebra. The bony substance extends inwards and constricts the notochord, outwards it permeates the vertebræ.

"In the caudal vertebræ, and perhaps in all the cervical vertebræ, the bony substance of the rings extends gradually to the surface of their centra. In the dorsal vertebræ, on the other hand, there is formed at the fifteenth day, independently of these rings, a broad though thin bony plate on the upper, and a second on the lower face of the centrum, with which the substance of the ring, as it extends, coalesces. The notochord at the eighteenth day may be seen traversing the intervertebral articular cavities like a thread."

Development of the Spinal Column of Mammalia.

Rathke, 'Schildkröten,' pp. 66, 67.—"In the pig and sheep the bony substance is deposited immediately around the notochord, in such a manner that, at first, as in birds, it forms a narrow and thin ring, from which it passes partly towards the surface, partly towards the ends of the separate centra, and after a time reaches the surface, but not the ends. To complete the centra, there arise in the latter two special disks of bone for each vertebra, which afterwards apply themselves to the previously ossified middle part, and wholly coalesce with it.

'In pig-embryos of 1 in. to 1 in. 3 lines in length, the notochord ran straight through the already existing rudiments of the intervertebral ligament like a delicate filament" (p. 77).

Bischoff, in his various works, shows that the earliest changes in the vertebral column of mammals are the same as in birds.

"In like manner as in the *Mammalia* and birds, the ribs in the *Chelonia* grow out as simple rays from the neural arches (*Bogenschenkeln*) of the vertebræ, quite close to their bodies. Very close to the places where they have arisen, however, the ribs of birds and mammals send, as a rule, a process downwards and inwards, which increases more or less in length and thickness, enlarges somewhat at its free end, and becomes closely applied thereby to one, or two, bodies of vertebræ, by the intermediation of the articular capsule which now becomes formed. This process is the neck and head of the rib."—Rathke, *Schildkröten*, p. 97.

"The cervical transverse processes of birds and *Mammalia* attain their forked form in quite a different manner from the ribs, namely, by the coalescence at one end, of what are properly two transverse processes which have grown out of the vertebra, while, on the other hand, a rib has become forked, because, though originally a perfectly simple ray, it has sent out a secondary process from one of its ends."

It results from the observations which have just been detailed, that with certain real or apparent exceptions which have been duly noted, there is a very great uniformity in the mode of development of the vertebral column in all *Vertebrata*.

The primary processes up to, and inclusive of, segmentation or division into somatomes, appear to be the same in all; and there is every reason to believe that the somatomes become differentiated in the same general way.[1] There seems to be no difference, save in degree, in the chondrification which takes place in the immediate neighbourhood of the notochord and in the neural and hæmal

[1] The relations of the ganglion to the rudiment of the rib and neural arch and segment of the dorsal muscles in the mouse's embryo are the same as in that of the bird.

arches. The intercentra correspond in fishes, as in *Amphibia* and birds, to the middle of each somatome; and it does not appear that they are, to any appreciable extent, produced by the metamorphosis of the notochord.

When ossification takes place, the diaphysis appears as a ring, or part of a ring, in immediate contact with, or very close proximity to, the notochord, which it usually embraces completely, though in the rare case of some *Amphibia*, only partially. The diaphysis then increases inwards so as to constrict the notochord, and outwards, so as to invade the centrum more and more. A distinct ossification is commonly formed in each neural arch, and one or more others in each hæmal arch.

In the higher or abranchiate oviparous *Vertebrata* there would seem to be no other centres of ossification in the vertebra than the five just mentioned, except those of the terminal epiphyses. In fishes, on the other hand, a distinct centre—which might be termed the *paraphysis*—is occasionally found in the paraphysial portion of the centrum.

The dorsal vertebræ of a young carp exemplify this structure remarkably well. The diaphysis is represented by an annular osseous ring, which surrounds the notochord and gives off a vertical median process or plate, and two inferolateral plates, which unite the hollow bony cones into which the osseous ring dilates in front and behind. The ossified neurapophyses expand into wedge-like lower ends, which embrace the vertical plate of the diaphysis, and whose apices come into contact with its annular part.

A thick cuneiform mass is interposed between the base of the neurapophysis and the inferolateral plate of the diaphysis on each side. The outer surface forms part of the general contour of the vertebra, and is not produced into a distinct process, though it represents a parapophysis, and gives attachment to the broad head of the distinctly ossified rib. The outer half of the mass is ossified as a distinct paraphysis; the inner in the young carp is still cartilaginous. In the adult the whole wedge-like paraphysial portion of the centrum is ossified; but, instead of becoming united with the diaphysis and neurapophysis, it is anchylosed with the rib, and seems to form its head. In the pike, the paraphysis, more or less produced into a parapophysis, remains distinct from both rib and diaphysis, and the latter occupies a very much larger share of the whole vertebra.

As I have said above, no distinct ossific centre appears to be developed in the paraphysial region of the centrum in any of the abranchiate *Vertebrata*; but it becomes ossified partly by the encroachment of the neurapophysial, and partly by that of the diaphysial, ossifications.

These two ossifications may coalesce so as to leave no trace of their primitive distinctness, as in *Ophidia*, *Lacertilia*, and birds; or as in mammals, *Crocodilia*, *Chelonia*, and many extinct reptiles, they may remain for a long time, or permanently, separated by a suture, which may be termed the "*neurocentral suture*."

It is very commonly assumed that this neurocentral suture is a sort of morphological landmark, and that it always indicates the boundary between the neurapophysis on the one hand, and the diaphysis or osseous centrum on the other; so that any process which is given off from the vertebra above the suture, is supposed to arise from the neurapophysis, while those given off below it only, are said to arise from the centrum.

It is only necessary to cite a few facts, which may be readily verified, however, to show that the neurocentral suture is of no value as a test of the nature of the parts above and below it.

In man and in the pig, the heads of the ribs, whether dorsal or cervical, are (as Retzius has well pointed out) articulated above the neurocentral suture ; and therefore, if we accept the ordinary definition, not to the centrum at all, but to the neurapophysis. Furthermore, if we accept the ordinary view, the "inferior transverse processes" in the neck of these animals are not parapophyses, but second diapophyses, inasmuch as they arise from the neurapophyses, and not rom the centrum.

The "transverse processes" of the lumbar vertebræ are usually given off above the neurocentral suture, and are therefore called "diapophyses." In a young Dugong, in the Museum of the Royal College of Surgeons, I find that, in the two hinder lumbar vertebræ, these transverse processes are given off below the neurocentral suture.

In the *Echidna* the head of every rib is attached to the centrum, or below the neurocentral suture ; and in the neck, this suture lies between the upper and lower transverse processes.

Thus, if we follow out logically the view that the neurocentral suture indicates the boundary between the neurapophyses and the centrum, and if we accept the current definition of diapophyses and parapophyses, we arrive at the conclusion, that, in the cervical region, man and the pig have vertebræ with two diapophyses and no parapophysis, while the monotreme has a parapophysis and a diapophysis on each side ; that, in the dorsal region, the ribs in man and the pig are connected only with the neurapophyses, while in the monotreme they articulate only with the centra ; that the transverse processes of the anterior lumbar vertebræ of the dugong are diapophyses, while those of the posterior ones are parapophyses !

The crocodile and some extinct reptiles, such as the *Ichthyosaurus*, whose ribs are throughout attached to the centra, afford still more striking instances of the confusion which would be produced by taking the neurocentral suture as a morphological boundary.

Müller has argued that it is a distinctive character of fishes to have the ribs attached to the centre of the vertebræ or to parapophyses, and his views have been adopted by other anatomists ; but the ribs of the *Ichthyosaurus* and of the *Echidna* are as completely and solely attached to their centra as those of any fish ; so that if we merely take the facts furnished by anatomy, the doctrine that there is anything peculiarly piscine in the attachment of the ribs to the centra only, falls to the ground.

But it may be urged that the connexion of the head of the rib with the centrum, in mammals and the higher *Vertebrata*, is secondary, that with the diapophysis being the primary and essential one. This is a very widely current doctrine, and it is sanctioned by Rathke, as we have seen in the passages quoted above, though they are not quite consistent with one another. It is with great hesitation that I venture to contravene the distinct statements of so eminent and accurate an embryologist as Rathke, but my own observations lead me to precisely the opposite conclusions.

In the spinal column of embryos of the mouse 7–8ths of an inch long, for instance, I find that the posterior dorsal vertebræ (A. fig. 10) have no diapophyses, and that the ribs have no tubercles, but that their heads pass directly into the cartilaginous substance of the centrum. Further forwards (B, C) both diapophysis and tubercle become more and more developed, until at length they come into contact and articulate in the ordinary way. Finally, in the cervical region (D) the rib and the diapophysis are, even in this early stage, confluent.

These facts are, I conceive, wholly at variance with the supposition that the

primary connexion of the ribs is with the diapophyses. On the other hand, they teach that the ribs in the mammal are, as in the fish, primarily continuous with the centre of the vertebræ—a result which is in perfect accordance with the ordinary embryological relations of the higher and lower animals.

The hæmapophysial cartilage passes off from the paraphysial cartilage on the one hand, just as the neurapophysial cartilage is given off from it on the other.

If the hæmapophysial cartilage becomes divided into rib and process, at some little distance from the centrum, the rib is said to be attached to a parapophysis ; and I believe that the only consistent definition that can be given of a parapophysis is, that it is developed from the proximal end of a hæmapophysial arch.

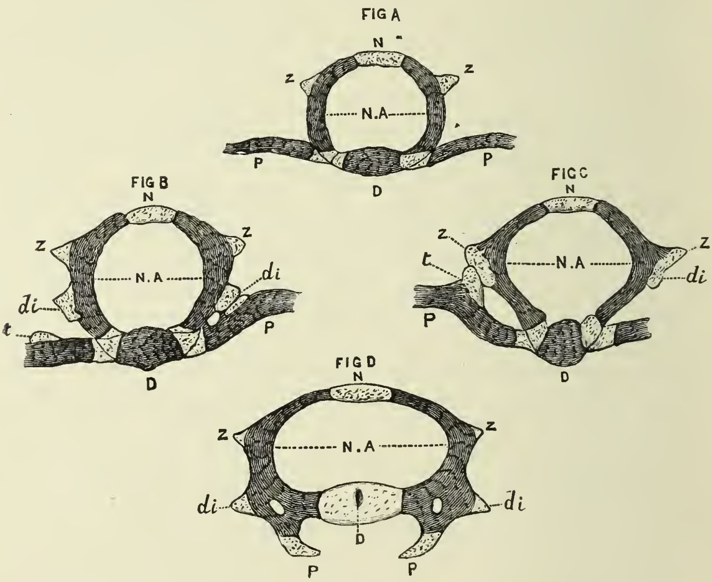


Fig. 10.—Vertebræ of an embryonic mouse $\frac{7}{8}$ths of an inch long. A. The penultimate dorsal vertebra. B. A middle dorsal ; and C′. an anterior dorsal vertebra. D. A posterior cervical vertebra. N. Metaneurapophysis or neural spine. N.A. Neurapophyses. Z. Zygapophysis. *di.* Diapophysis. P. Rib or pleurapophysis. *t.* Its tubercle. D. Diaphysis. The ossified parts are shaded, the cartilaginous, dotted.

If the paraphysis is merged in the general body of the vertebra, and the rib becomes distinctly articulated close to it, the attachment of the rib is said to be to the centrum.

If the paraphysis is bent upwards, so as to pass insensibly in direction into the neurapophysis, and becomes ossified in continuity with the latter, the head of the rib is said to be attached to the neurapophysis, although, in truth, the head of the rib, or at any rate the proximal end of the hæmapophysial arch of which that rib is a part, always retains, so far as we have any evidence, its primitive connexion with its vertebral centrum, into whatever new ones it may enter.

If the neurocentral suture does not define the lower limits of a neurapophysis, and if the true definition of a parapophysis is that given above, it is obvious that

our nomenclature of the parts of the dorsal and lumbar vertebræ throughout the vertebrate series, requires a thorough revision.

To this subject I hope to return on a future occasion.

VII.—I subjoin the views of Vogt, and the criticisms of the late great anatomist Johannes Müller upon them, as the best means of exhibiting their relation to those I have advocated.

" If we ask ourselves what we mean by vertebræ, the primary segments of the still indifferent tissue round the chorda, which arise in all vertebrate embryos, are the first things to suggest themselves. These persist only in the lowest grades of vertebrate animals, while in the higher they disappear, in consequence of the more and more complete development of secondary organs, especially of the extremities ; so far as we are able to trace these segments, so far is there a formation of vertebræ.

" But there is at once a difficulty, when we endeavour to find these segments in the rudiment of the skull of any vertebrate embryo. It is true that many inflexions may be observed which appear to correspond with such vertebræ, but unfortunately these do not appear in the same places in different embryos ; and besides, these inflexions and curvatures of the base of the skull are not in the least similar to the sharply and clearly defined intervals between the primary vertebræ. The first of these intervals is always formed behind the auditory vesicles, and lies therefore between the occiput and the first cervical vertebra ; further forwards, as has been said, no such interval is discoverable. But in the Cyclostome fishes, which represent this embryonic condition, no vertebral divisions of the skull are discernible ; in fact we have in the Myxinoids, only the chorda with its sheath and muscular and cutaneous vertebral rings, which are repeated up to the skull, but there cease. The skull of the Myxinoids, like that of the higher cartilaginous fishes, cannot by any amount of violence be forced under the vertebrate type. In the skull, then, the primary vertebral segments are wanting. However, they might be obliterated by the early development of the organs of sense, or by the aberrant development of the brain.

" But there remains a second means of discovering the cranial vertebra, by examining the solid cartilaginous and bony basis of the skull ; though here also we meet with insuperable difficulties. As the primitive type of the more solid bodies of the vertebræ, we have everywhere cartilaginous rings arising out of the sheath of the chorda, and deposited around its nucleus. Whether they arise as lateral halves or as entire rings, whether they embrace the chorda completely or only above or below, is a matter of no essential moment. But are such cartilaginous rings deposited around the chorda, discoverable in the skull ? They will be sought for in vain unless it be in the last, occipital, cranial vertebra ; in this we still find all the characters of a vertebra—the investment of the chorda, the chondrification in the sheath of the chorda. But the chorda does not pass into the so-called first and second cranial vertebræ ; it invariably ends, as Rathke justly states, between the auditory capsules, and never passes into the body of the second cranial vertebra, let alone that of the first. The lateral cranial trabeculæ, which bear the two anterior cranial vertebræ, can by no possibility be regarded as centra of vertebræ, since in this case the characteristic feature, the being traversed by the chorda, is entirely absent. Again, these lateral trabeculæ are continued uninterruptedly forwards, below the first division of the brain, showing no trace of a median division. But in what part of the vertebral column has it ever been seen that two vertebræ arise united and afterwards divide ?

" It has therefore become my distinct persuasion that the occipital vertebra is

indeed a true vertebra, but that everything which lies before it *is not fashioned upon the vertebrate type at all*, and that all efforts to interpret it in such a way are vain ; that therefore, if we accept that vertebra (occipital), which ends the spinal column anteriorly, there are no cranial vertebræ at all."—Vogt, *Entw. d. Geburtshelferkröte*, pp. 98–100.

"Vogt, and in the present work Agassiz also, contest the justice of the theory of the composition of the skull of several vertebræ, and will only admit an occipital vertebra, because the embryonic chorda, according to Vogt's investigations, extends no further in the skulls of fishes and *Amphibia*. In this, in my opinion, too much stress is laid upon a single result of embryological investigation. That, however, the chorda in the frog's larva extends beyond the base ot the occiput, further than where the slight trace of the basioccipital is ultimately formed, I have myself seen. Even the anterior part of the vertebral column of the Rays shows that the chordal system, out of which, according to my own and Vogt's observations, only the central part of the fishes' vertebra proceeds, may be abortive, whilst the cortical part of the vertebra, which arises in quite a different way, is at its maximum of development. In a longitudinal section of the anterior part of the vertebral column of a Ray, it is seen that the central parts of the vertebræ, in the axis of the vertebral column, or those parts which are developed from the chordal sheath alone, become finer and finer anteriorly (although the column still exhibits vertebral divisions), and at last cease entirely, without reaching the anterior end of the vertebral column. On the other hand, *Branchiostoma lubricum* shows us the opposite extreme ; the chorda passes beyond the anterior end of the skull, beyond the mouth and the eyes, far into the extremest end of the snout.

"This remarkable fact, first observed by Sundevall, was very surprising to me, since in consequence of my studies up till that time, I regarded the existence of three vertebræ in the proper cerebral cranium as certain, at least I considered the assumption of a fourth ethmoidal vertebra to be uncertain and undemonstrated.

"For now I saw at once, that it was undoubtedly possible that the cephalic vertebral column might extend further forwards. There need not always be three cranial vertebræ developed in the head ; in birds, reptiles, and fishes, the most anterior vertebra is abortive, and is even entirely wanting in some families ; but, in the *Mammalia* and man, three cranial vertebræ are without exception discoverable in the basis cranii, either in the fœtus, or in many cases even in young or middle-aged animals—the occipitale basilare, sphenoideum basilare, posterius and anterius ; these also occur in fish. How far the chorda primitively extends in *Mammalia* is not yet made out ; but even although it should not reach through the whole basis cranii, this, from the reasons which have been stated, would be no good argument."—Joh. Müller, *Bericht.* cclxviii–ix., Müller's *Archiv*, 1843.

END OF VOL. I.

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